Indicators of Benthic Biodiversity for the Eastern Scotian Shelf

L. Henry, E. Kenchington, D.C. Gordon, Jr.,
K. MacIsaac and C. Bourbonnais

Science Branch
Maritimes Region
Department of Fisheries and Oceans
Bedford Institute of Oceanography
PO Box 1006
Dartmouth, Nova Scotia B2Y 4A2

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ABSTRACT

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As part of ecosystem inititatives to identify useful indicators to help monitor and maintain benthic marine biodiversity on the Eastern Scotian Shelf, the Ocean Branch of the Canadian Department of Fisheries and Oceans funded work into the measurement and evaluation of various measures of biodiversity. The last 10 years has been marked by much research into the benthic habitats and biodiversity of the Eastern Scotian Shelf, particularly during mobile bottom fishing gear impact studies. Databases available at the time for benthos collected by videograbs and epibenthic sleds on Western Bank, Emerald Bank, Sable Island Bank and Banquereau were used to estimate values of commonly used structural and functional indices. The potential utility of each indicator was judged on its ability to detect differences in benthos at fine scales (within a bank) and across large areas (across banks) on the Eastern Scotian Shelf, the reliability of the estimated value, and the experimental considerations needed to obtain its measurement. Genetic indicators were discussed, but not evaluted here as there were limited molecular analyses of non-commerical benthos for this region. Indicators of species richness and heterogeneity, phylogenetic composition and biogenic complexity reliably detected differences in benthic biodiversity at both spatial scales. It was recommended that manipulations of existing databases to generate taxonomically more coarse information should be undertaken to determine whether indicator sensitivity requires species-level (and therefore much taxonomic effort) to detect differences. Phylogenetic differences in phylum biomass composition detected significant differences between banks, and further research should be done to evaluate processes that structure biodiversity and make the benthic communities of these banks so distinct from one another. Until genetic analyses become routinely more feasible, it was recommended that molecular analyses on non-commercial benthos be performed opportunistically, on species at risk and biogenic organisms.

RÉSUMÉ

Henry, L., E. Kenchington, D.C. Gordon, Jr., K. MacIsaac and C. Bourbonnais. 2002. Indicators of Benthic Biodiversity for the eastern scotian shelf. Can. Tech. Rep. Fish. Aquat. Sci. 2433: ix + 61 p.

La section Océans du Département canadien des Pêches et Océans a financé des études de mesures et d'évaluation de mesures de biodiversité dans le cadre d'initiatives écosystemiques qui visent à identifier des indicateurs utiles de surveillance et de maintien de la biodiversité sur la partie est du plateau néo-écossais. Les dix dernières années ont été marquées par des recherches intensives sur les habitats benthiques et sur la biodiversité du plateau, particulièrement lors des études d'impact des engins de pêche de fond mobiles. Des banques de données alors disponibles pour la faune benthique échantillonnée par vidéograbs et par planeurs sous-marins épibenthiques sur le banc Western, le banc d'Émeraude, le banc de l'Île de Sable et le banc Banquereau ont été utilisées pour estimer les valeurs d'indices structuraux et fonctionnels couramment utilisés. L'utilité potentielle de chaque indicateur a été estimée par sa capacité à détecter des différences dans le benthos à une échelle fine (à l'intérieur d'un même banc) et à une échelle plus large (entre les bancs) sur la partie est du plateau néo-écossais, par la fiabilité des valeurs estimées, et par les conditions expérimentales nécessaires pour obtenir ces mesures. Les indicateurs génétiques ont été discutés, mais non évalués dans ce rapport en raison des analyses moléculaires limitées pour les espèces benthiques non-commerciales de la région. Les indicateurs de richesse en espèces et d'hétérogénéité, la composition phylogénétique et la complexité biogénique ont détecté des différences fiables dans la biodiversité benthique aux deux échelles. Il est recommandé de manipuler les banques de données existantes afin de générer des informations taxonomiques moins fines et de déterminer si les indicateurs de sensibilité nécessitent des données au niveau de l'espèce (ce qui demande un effort taxonomique supplémentaire) pour détecter des différences. Les différences phylogénétiques dans la composition de la biomasse d'un phylum permettent de détecter des différences significatives entre les bancs et des recherches supplémentaires devraient être entreprises pour évaluer les processus qui structurent la biodiversité et font que les communautés benthiques de ces bancs soient si distinctes les unes des autres. Jusqu'à ce que les analyses génétiques deviennent plus communes, il est recommandé que les analyses moléculaires soient entreprises sur le benthos non-commercial de façon opportuniste, sur les espèces en danger et sur les organismes qui supportent la vie d'autres organismes, des animaux biogéniques.

INTRODUCTION

A general definition for "biodiversity"

An important objective of any marine ecosystem management framework is to support the maintenance of biological diversity in light of increasing human pressures on the oceans. "Biodiversity" encompasses the entire scale of life from the level of the gene to entire ecosystems. Maintaining biodiversity in marine environments first requires an understanding of natural processes that produce spatial and temporal variations in marine gene pools, species assemblages, functional groups, populations, communities and ecosystems.

Variation in marine biodiversity is structured by many natural processes acting at all spatial and temporal scales (Willis and Whittaker 2002). For example, a combination of random mutations and selection at the level of the gene creates genetic biodiversity at scales of thousands of years (Skibinski 2000). The feeding and movements of macrofauna create sediment deposits that provide habitat for diverse meiobenthic assemblages (Austen et al. 1998). Depth-dependent ice-scour prevents monopolization of substrates by overgrowth competitors in the shallow substidal, keeping diversity levels relatively lower than those at deeper depths (Barnes et al. 1996).

One method for assessing whether management plans have succeeded or failed in maintaining biodiversity is the use of biological "indicators". Indicator values are compared to reference points, from which estimated values are judged as "acceptable" or "unacceptable". The most meaningful indicators are those sensitive enough to human ocean activities to allow the effects of these activities to be distinguished from underlying natural processes.

In June 2000, a workshop on ecosystem considerations was held to discuss the incorporation of ecosystem-based management for the Eastern Scotian Shelf Integrated Management (ESSIM) area (O'Boyle 2000). Patterns in benthic biodiversity are not well known on the Eastern Scotian Shelf (or indeed in most managed areas). Some benthic databases now exist for this region, and much syntheses are provided in Gordon and Fenton (2002) and Stewart et al. (2001). Further effors are required, however limited the data may be to begin an evaluation of potential biodiversity measures.

The geographical area of the Eastern Scotian Shelf encompasses several ecosystem types including submarine canyons, continential slopes, gravel-bottom and sandy-bottom habitats. Geographic patterns in biodiversity are hard to predict as the distribution of benthic fauna depends on physico-chemical factors that differ across these ecosystem types, e.g., substrate types, bottom current velocity, as well as biological factors, e.g., competition for space, predation, food type and availability and the life histories of the species themselves (e.g., fast-growing, quick sexual maturation, short life-span versus a slow-growing, perennial species with a long lifespan). Thus, large scale shelf-wide differences (i.e., spatial variations at a scale of thousands of kilometres) and

intermediate scale bank-wide differences (i.e., variation at a scale of hundreds of kilometres) in patterns of benthic biodiversity are expected to occur.

Understanding benthic biodiversity on the Eastern Scotian Shelf is complicated by the potential effects of planned human ocean activities in the ESSIM area. Resource exploration, tourism, fisheries, naval exercises, marine transportation and pollution are likely to affect ecosystem structure (e.g., biomass, species richness and composition) and function (e.g., trophic functions, growth, mortality, larval recruitment processes) in the ESSIM area by altering ecosystem environmental conditions such as substrate, physico-chemical sediment properties, respiration of benthos, predation and mortality. At larger spatial and temporal scales, the effects of global warming could also impact benthic biodiversity patterns by changing circulation patterns, water temperature and salinity.

The ESSIM initiative identifies the critical need for information regarding useful criteria (i.e., indicators) by which the effectiveness of management plans to maintain biodiversity can be measured. Until recently, there had been little synthesis into determining how species diversity is impacted by human ocean activities in Atlantic Canada (but see Brylinski et al. 1994, Prena et al. 1999, Kenchington et al. 2001, Gordon et al. 2002). No studies have been conducted anywhere on the Scotian Shelf that examined how genetic biodiversity of non-commerical benthic invertebrate species is affected by human ocean activities. Most efforts to evaluate genetic variation in benthic assemblages from the Eastern Scotian Shelf have focused on commercially valuable species such as lobsters, sea scallops, clams and sea urchins. Furthermore, management efforts to implement activities such as environmental impact assessments and current integrated fishery management plans, e.g., those outlined in O'Boyle (2000), for fisheries-related activities simply do not address ecosystem issues like species diversity and genetic variability in non-commercial benthos such as sponges, corals, hydroids and bryozoans that provide habitat for commercial species e.g., lobster (*Homarus americanus*) (Wahle and Steneck 1992), herring (*Clupea harengus*) (Reid et al. 1999), plaice (*Hippoglossoides platessoides*) (Johnson et al. 1999), cod (*Gadus morhua*) (Tupper and Boutilier 1995), haddock (*Melanogrammus aeglefinus*) (Cargnelli et al. 1999a), ocean pout (*Macrozoarces americanus*) (Steimle et al. 1999), pollock (*Pollachius virens*) (Cargnelli et al. 1999b) and Acadian redfish (*Sebastes fasciatus*) (Pikanowski et al. 1999).

Project outline

The need to identify indicators of benthic biodiversity for the ESSIM area *sensu* O'Boyle (2000) stimulated the present study. Funding was provided by the Oceans Branch Applied Science Fund of the Canadian Department of Fisheries and Oceans. The intent of this report was to provide ocean managers of the ESSIM area with recommendations for useful indicators of benthic biodiversity and methods for their estimation as preliminary steps in meeting various elements of the Precautionary Approach Framework for ESSIM initiatives *sensu* O'Boyle (2000) to identify indicators of ecosystem change and to maintain biodiversity.

This was achieved by examining whether commonly used biodiversity indicators could detect differences in benthic biodiversity across large ("shelf-wide") and intermediate ("bank-wide") spatial scales. Few benthic datasets were available at the time to permit evaluating the usefulness of indicators on temporal scales. At the time of data analysis for this report, several datasets were available that pertained to benthos sampled from 4 different banks, each collected within a relatively smaller area on each bank. This close clustering of benthic sampling effort prevented detailed characterization of benthic communities on a bank, but it permitted the evaluation of potentially useful indicators to detect differences across a fine scale on that bank. The abilities of indicators to detect bank-wide differences were conservatively extrapolated from their capacities to detect differences at these finer, more localized scales (i.e., at the scale of tens to hundreds of metres).

Results were summarized by rating each indicator according to its ability to detect differences at large and smaller scales, the accuracy with which the indicator value was estimated, and the experimental effort and cost required for its measurement. Commonly reported indices of genetic biodiversity and their sensitivities to natural processes and human ocean activities were discussed separately as there were no genetic data from the ESSIM area at the time to evaluate the effectiveness of using such indicators for non-commerical benthos. General recommendations were summarized at the end of this report to provide ocean managers with suggestions regarding the estimation of biodiversity indicators and the practicality of using indicators as management tools in the ESSIM area. The findings of this report were considered in three main sections:

(1) Part I reported on the ability for commonly used biodiversity indicators (i.e., measures of species richness, indicator taxa, phylogenetic differences and heterogeneity) to detect differences across banks of various bottom types in the ESSIM area i.e., sandy (Banquereau), gravel (Western Bank), gravel and sand (Sable Island Bank) and gravel, muddy, sandy (Emerald Bank). The ability for indicators to detect differences at small spatial scales was reported for benthos on Western Bank as the database for this area was the most detailed at that time.

(2) Part II summarized results of Part I by considering the utility of each indicator based on several criteria: indicator sensitivity to detect differences across various spatial scales, the reliability of estimated values, and experimental design considerations necessary for its measurement.

(3) Part III examined various indicators of genetic biodiversity. Potential effects of natural processes and human ocean activities on genetic biodiversity in marine invertebrates are considered. Much attention was dedicated to how physical disturbance could affect genetic variability in colonial organisms such as sponges, corals, bryozoans and hydroids that contribute to three-dimensional habitat complexity and ultimately fisheries production and benthic biodiversity in marine environments.

INDICATORS OF BENTHIC BIODIVERSITY

The effectiveness of any ecosystem initiative to address conservation priorities depends on the existence of adequate databases on species diversity i.e., the number of species (species richness) and the proportional abundance of species (heterogeneity diversity) within a management area (Gray 2000). Another approach to address these needs is to use indicator species (i.e., individual species with particular life history traits that are associated with certain habitats) to measure and monitor biodiversity. This methodology reduces benthic sampling intensity and analytical effort because fewer taxa need to be resolved and included in the databases.

Species richness, heterogeneity and indicator species are measures of "structural" biodiversity, and indicate how an assemblage appears to observers. "Functional" biodiversity indicates how an assemblage operates e.g., functional guilds (e.g., predators, herbivores, omnivores) and biogenic structures (i.e., a biological structure, such as erect tubes of arborescent branches that contribute habitat to other organisms). These measures of benthic biodiversity can be used in conjunction with structural diversity indices as criteria to determine whether ecosystem objectives are met to prevent the extinction of species and the introduction of new ones in the ESSIM area.

Benthic surveys on the Eastern Scotian Shelf

During surveys to establish appropriate locations for mobile fishing gear experiments, DFO collected benthos from various outer banks on the Eastern Scotian Shelf: Western Bank, Emerald Bank, Banquereau and Sable Island Bank. These banks were described below (also see Fig. 1 and App. I for detailed site and station data), while benthic sampling protocols were briefly described for each area. Sampling gear has been described in detail by Prena et al. (1996, 1999) and Rowell et al. (1997).

Western Bank

Western Bank is a relatively shallow area at about 70 metres depth that lies between Sable Island Bank and Emerald Bank on the outer Eastern Scotian Shelf. Most of Western Bank is contained by the 4TVW haddock nursery box that has been closed to most groundfishing since 1987. Bottom sediments on Western Bank are variable, consisting of finely to coarsely grained sand and gravel. Surficial sediments are typically Sable Island sand and gravel derived from the reworking of glacial debris, containing little silt and clay particles (Fader et al. 1977).

Benthos were obtained in September 1997 during surveys on a primarily gravel bottom about 70 metres deep from the C.S.S. *Parizeau* (Cruise P97-053, Fig. 1, site A, App. I). Seventeen $0.5m^2$ videograbs (described in Rowell et al. 1997) were used to capture images of the bottom and associated fauna within each of 4 parallel 2 kilometre long corridors ("B", "E", "G" and "I"), as well as to sample benthos and sediments.

Emerald Bank

Emerald Bank is a relatively shallow area about 85 metres deep that lies just west of Western Bank. Typical bottom substrate is mixed Sable Island sand with more than 50% gravel.

Twelve benthic samples were collected with a $0.5m^2$ videograb and an epibenthic 0.34 metre sled (described in Rowell et al. 1997) at 2 sites approximately 85 metres deep during June 1996 from the C.S.S. *Parizeau* (Cruise P96-009, Fig. 1, site B, App. I).

Banquereau

Banquereau is the largest, easternmost bank in the ESSIM area. Most of the bottom substrates on Banquereau are comprised of Sable Island sand facies with less than 50% gravel (Lawrence et al. 1985). The shallowness of this bank at around 70 metres, its proximity to the edge of the Scotian Shelf and variable current flows make Banquereau a highly dynamic bank. These hydrodynamic factors are largely responsible for the formation of sand ridges, ripples and accumulations of clam shell debris in the valleys of these ripples (Lawrence et al. 1985). These formations could have direct consequences for the recruitment and distribution of benthic invertebrates in this area.

Benthos were obtained in May 1998 during surveys on a primarily sandy-bottom clam bed, about 75 metres deep from the C.C.G.S. *Hudson* (Cruise H98-015, Fig. 1, site C, App. I). Thirty $0.5m^2$ videograbs (described in Rowell et al. 1997) were obtained, simultaneously capturing images of the bottom and associated fauna.

Sable Island Bank

Much of this bank lies south of Sable Island, a land mass that rises about 26 metres above sea level on the Eastern Scotian Shelf. Sable Island Bank is separated from Banquereau by a large, deep submarine canyon known as the Gully that has stimulated much research interest (see syntheses provided by Gordon and Fenton 2002). Like Banquereau, most of the bottom on Sable Island Bank is comprised of Sable Island sand facies with less than 50% gravel, although shell debris is commonly mixed with these sediments closer to the centre of the bank (Lawrence et al. 1985). Sable Island Bank is also a highly dynamic environment, and disturbance caused by constantly shifting sediments may have consequences for the distribution of certain organisms (e.g., infaunal invertebrates).

Ten benthic samples were obtained with a $0.5m^2$ videograb (described in Rowell et al. 1997) during June 1996 at about 46 metres depth near Panuke from the C.S.S. *Parizeau* (Cruise P96-009, Fig. 1, site D, App. I).

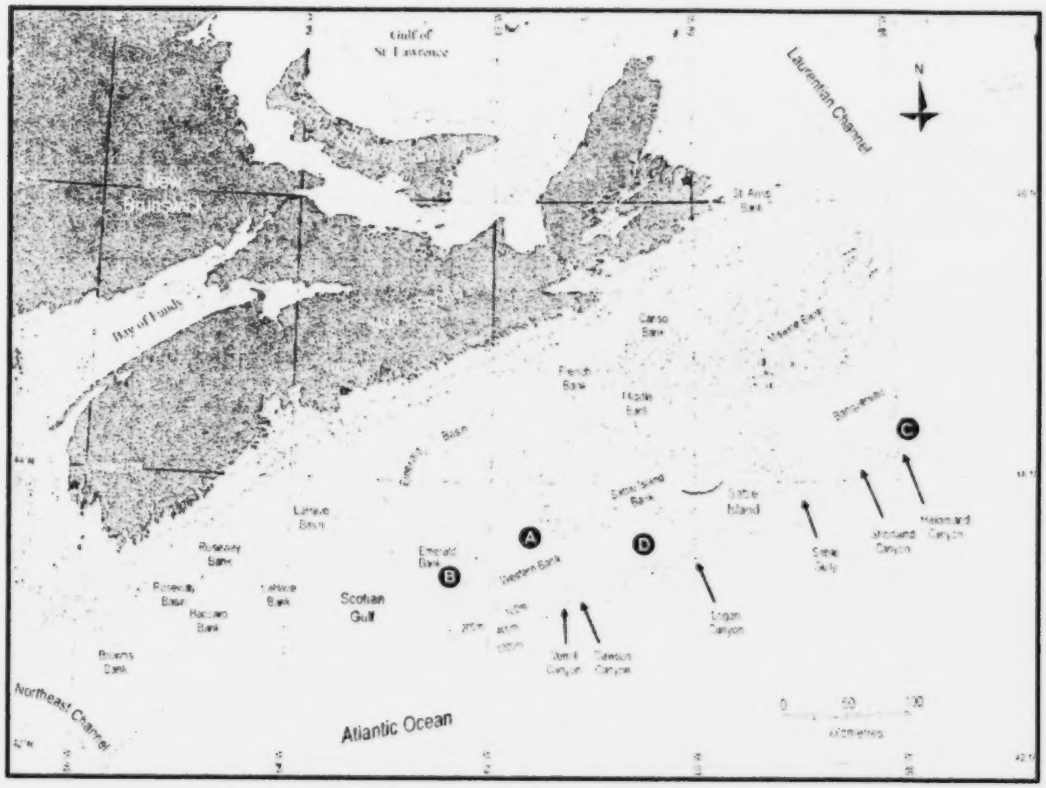

Figure 1. Map of sampling locations on the Eastern Scotian Shelf.

Indicators of structural species diversity - species richness

Species lists

Species checklists indicate the habitats present in an area, environmental quality and even the extent to which knowledge of biogeographical patterns in biodiversity is being enhanced (Costello 2000). Short and long-term community shifts, rates of species extinction and colonization can be described simply by presence/absence data. The ease with which changes to species lists within the ESSIM area could be measured makes these checklists valuable management tools to monitor and conserve benthic marine biodiversity. Yet the initial acquisition of checklists for a given area requires that most species have been sampled, and that their taxonomic identifications were correctly and reliably obtained e.g., a change in taxonomic staffing did not result in altered identifications. These requirements will undoubtedly be time consuming, especially when few trained taxonomists are available to identify taxa.

The recently developed European Register of Marine Species outlined by Costello (2000) could serve as a model database of species lists for the Eastern Scotian Shelf to facilitate the monitoring and protection of marine biodiversity in this management area. At the time of this analysis, the taxonomic benthos database from Western Bank in 1997 was the most complete: a species checklist was provided in Appendix II.

Most studies of benthic marine diversity include at least one measure of species richness to define the number of species in a unit of space. Whittaker (1972) recognized that species richness could be measured at four different scales: point diversity (i.e., a single sample), alpha (α) diversity (i.e., several samples within a habitat, where point diversity=α diversity when sample size equals one), beta (β) diversity (i.e., between habitat diversity) and gamma (δ) diversity (i.e., over an entire landscape).

Indices of α-diversity are based on the relationship that exists between the number of observed species (**s**) and the number of individuals observed (**n**).

Margalef's index

One of the most widely used diversity measure is Margalef's index (Margalef 1958), commonly estimated as:

$$D = \frac{s-1}{\log_{10}(n)}$$

Menhinick's index

Menhinick's index (Menhinick 1964) is empirically related to Margalef's index, and is estimated as:

$$D = s / \sqrt{n}$$

Both indices increase in value with more observations of new species from fewer individuals. **D** also varies with sample size **n** as well as with the number of observed species **s**. Unless the functional relationship between **s** and **n** is truly constant (i.e., related by a constant **k**), species richness **D** will vary with **n** (Peet 1974). Sample area (**A**) could be used instead of sample size **n**, but Margalef's and Menhinick's indices assume that the relationship between **s** and **A** are related by a constant **k**. This condition seems unlikely to be the case for benthos that exhibit highly patchy distributions patterns. Alternatively, measures of species richness could be obtained from samples of equal size (i.e., the number of individuals sampled remained constant) to circumvent problems associated with the unknown relationship between **s** and **n**.

Rarefraction curves

Both the number of species observed **s** and the overall number of species **n** often vary between benthic sampling. Recall that both Margalef's and Menhinick's indices are biased where sample sizes of **n** or **s** are unequal. This bias can be removed using a statistical method called "rarefraction" to measure species richness (Hurlbert 1971). The underlying model computes the expected number of species [E (S_n)] in a random sample of size **n** as the sum of all probabilities that all species are included in that sample, so that:

$$[E(S_n)] = \sum_{i=1}^{s} \left\{ 1 - \left[(N-n_i)/n \; / (N/n) \right] \right\}$$

The function represented by $[E(S_n)]$ yields a distinct curve for each assemblage, so that species richness can be estimated at any sample size **n**. As assemblage biodiversity increases, the curve is steeper and more elevated.

Rarefraction curves predict similar species richness estimates across assemblages even when the number of species and their respective relative abundances vary greatly between these assemblages (Peet 1974). Any conclusions derived under these conditions should be interpreted cautiously if no estimates of abundance were provided. Rarefraction curves can also lead to overestimating species richness when distributions are not random. Alternatively, Gray (2000) recommended calculating species accumulation curves for randomized samples to ensure that confidence intervals around the means are known.

Information measures of biodiversity relate to the uncertainty involved in making predictions about the next species to be encountered in a sample (Margalef 1958, MacArthur 1965, Lloyd et al. 1968). Indices that incorporate both elements of species richness and relative species abundance (i.e., "evenness" measures) are derived from information theory (Mouillot and Leprêtre 1999) and are also called "heterogeneity" measures (Peet 1974). However, without first describing species richness and evenness

independently, the relative importance of each parameter to the final heterogeneity measure is unknown. For example, the same heterogeneity estimate would be obtained from a sample in an assemblage with high species richness and low evenness as it would be from a sample in an assemblage with low species richness and high evenness. Heterogeneity indices should always be presented with richness and evenness estimates (Lloyd et al. 1968).

Variation in species richness indices across banks

The mean number of species **s**, Margalef's and Menhinick's indices were reported strictly for videograb samples collected on 4 banks of the Eastern Scotian Shelf (Tables 1-3).

Table 1. Mean number of species per grab across banks.

Bank	Sample size	Mean	Standard deviation
Western	17	109.412	16.008
Emerald	8	48.500	19.885
Banquereau	30	63.567	8.211
Sable Island	10	34.400	8.356

Table 2. Margalef's index across banks.

Bank	Sample size	Mean	Standard deviation
Western	17	109.075	16.023
Emerald	8	48.074	19.954
Banquereau	30	63.194	8.218
Sable Island	10	33.968	8.357

Table 3. Menhinick's index across banks.

Bank	Sample size	Mean	Standard deviation
Western	17	3.528	0.477
Emerald	8	2.819	0.308
Banquereau	30	2.872	0.347
Sable Island	10	2.410	0.893

There were a couple of interesting points to consider from these analyses. First, Western Bank had higher richness according to all indices. High biodiversity on this bank could be related to the abundance of rocky substrates that increase habitat heterogeneity and thus the availability of benthic microhabitats. Second, if Western Bank is excluded, there was little variation in values across Banquereau, Emerald and Sable Island Bank. Although these indicators did not consistently detect large scale differences in benthic biodiversity across banks, all three indicators detected the highest benthic biodiversity on

Western Bank relative to the other areas. When Western Bank is excluded from the analyses, the relative stability of indicator values over larger spatial scales prompted further examination into whether these banks were actually characterized by the same fauna, or whether similar values were simply obtained because of stable **s** and **n** ratios. This question was answered by examining the phylogenetic differences across banks in Section 2.2.

Variation in species richness indices within a bank

The species richness indices described and measured above were also reported here to examine their effectiveness in detecting differences at a fine spatial scale i.e., over a small area on Western Bank (Tables 4-6).

Table 4. Small-scale differences in the mean number of species.

Corridor	Sample size	Mean number of species per grab	Standard deviation
B	2	108.500	20.506
E	10	108.700	17.820
G	3	111.000	7.550
I	2	111.500	26.163

Table 5. Small-scale differences in mean Margalef's values.

Corridor	Sample size	Mean	Standard deviation
B	2	108.158	20.528
E	10	108.360	17.841
G	3	110.680	7.538
I	2	111.159	26.170

Table 6. Small-scale differences in mean Menhinick's values.

Corridor	Sample size	Mean	Standard deviation
B	2	3.680	0.110
E	10	3.582	0.339
G	3	3.091	0.850
I	2	3.764	0.626

The relative spatial stability of all indicator values probably limits their utility to detect small scale differences within a bank.

Phylogenetic differences across banks

Recall from Section 2.1.5 that benthic species richness was relatively stable across banks, with the exception of Western Bank (Tables 1-3). Detailed examinations of the

benthic faunal composition revealed that although s, Margalef's and Menhinick's indices did not greatly differ, these assemblages were comprised of very different taxa.

From data available at the time of these analyses, banks were distinguished by their biomass levels of different benthic taxa. Emerald Bank was largely represented by six phlya: Annelida, Mollusca, Arthropoda, Echinodermata, Nemertea and Sipuncula. In close geographic proximity to Emerald Bank is Western Bank, and this area was dominated by eight phyla: Annelida, Mollusca, Arthropoda, Echinodermata, Nemertea, Chordata, Cnidaria and Brachiopoda. Sable Island Bank was chiefly comprised of five phyla: Annelida, Mollusca, Arthropoda, Echinodermata and Nemertea. Banquereau was primarily made up of three phyla: Annelida, Mollusca and Arthropoda.

Molluscs and sometimes annelids tended to dominate benthic biomass on banks from the Eastern Scotian Shelf (Tables 7-8).

Table 7. Mollusc biomass across banks.

Bank	Sample size	Mean biomass (mg)	Standard deviation
Western	17	287 026.7 (83% of total biomass)	241 901.2
Emerald	8	16 165.8 (47% of total biomass)	23 594.0
Banquereau	30	1 121 801.8 (84% of total biomass)	413 509.9
Sable Island	10	177 569.7 (93% of total biomass)	253 705.6

Table 8. Annelid biomass across banks.

Bank	Sample size	Mean biomass (mg)	Standard deviation
Western	17	28 517.9 (8% of total biomass)	11 519.3
Emerald	8	10 421.6 (30% of total biomass)	5 293.2
Banquereau	30	15 627.8 (1% of total biomass)	8 743.3
Sable Island	10	10 069.9 (5% of total biomass)	12 136.5

Mean mollusc biomass was highest on Banquereau, but was proportionally greatest on Sable Island. Annelid biomass was highest on Western Bank, but proportionally dominated the biomass on Emerald Bank. These differences in faunal distributions were sufficiently strong to suggest the potential utility of phylogenetic community variation as an indicator of biodiversity at large spatial scales i.e., between banks. Their abilities to detect finer scale variations in benthic biodiversity was demonstrated by the large standard deviations of each estimate, although this limited the reliability of estimating a mean biomass value. As species data become available for all banks, it would be valuable to examine substrate-fauna affinities to explain these associations.

Taxonomic separation of banks

The ability to detect differences across banks in phylum biomass was evaluated using various procedures with PRIMER version 5.2.2 software (Clarke and Gorley 2001). Taxonomic composition according to phylum biomass was evaluated with multidimensional scaling (MDS) methods on raw biomass data compiled to date (Fig. 2). The similarity between banks was tested statistically with the analysis of similarity (ANOSIM) method by comparing banks pairwise with each other (Table 9).

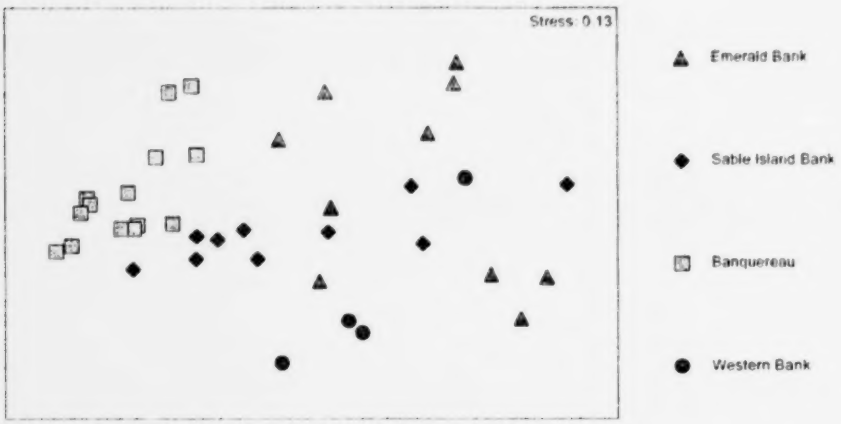

Figure 2. Taxonomic separation of banks according to phylum biomass

Table 9. ANOSIM results of pairwise comparisons between banks.

Pairwise groups	R-statistic	P-value
Emerald Bank, Sable Island Bank	0.343	0.002*
Emerald Bank, Banquereau	0.852	0.001*
Emerald Bank, Western Bank	0.195	0.070
Sable Island Bank, Banquereau	0.521	0.001*
Sable Island Bank, Western Bank	0.497	0.004*
Banquereau, Western Bank	0.982	0.003*

(* indicates statistically significantly differences in phylum biomass between a bank pair at α=0.05).

The MDS (Fig. 2) of these areas separates these sites into distinct areas in terms of phylum biomass. In most cases, the ANOSIM p-values are significant, although phylum biomass was not significantly different between Emerald and Western Banks.

The SIMPER procedure was performed to examine which phyla contributed most to the percent dissimilarity between banks (Table 10).

Table 10. SIMPER results. Cum. %=cumulative percent contribution of a phylum to the overall difference between banks, up to approximately 90%.

Emerald Bank & Sable Island Bank

Phylum	Emerald Bank mean biomass (mg)	Sable Island Bank mean biomass (mg)	Cum. %
Echinodermata	7 192	522	18.26
Annelida	10 076	10 070	32.77
Mollusca	17 507	177 570	46.25
Cnidaria	1 159	134	57.92
Sipuncula	67	0	69.36
Chordata	441	140	80.01
Nemertea	234	915	87.21
Arthropoda	276	610	93.48

Emerald Bank & Banquereau

Phylum	Emerald Bank mean biomass (mg)	Banquereau mean biomass (mg)	Cum.%
Annelida	10 076	5 713	23.14
Echinodermata	7 192	372	42.16
Mollusca	17 507	912 910	55.01
Chordata	442	1	65.30
Sipuncula	67	7 706	75.16
Cnidaria	1 159	26	84.83
Nemertea	234	377	91.79

Sable Island Bank & Banquereau

Phylum	Sable Island Bank mean biomass (mg)	Banquereau mean biomass (mg)	Cum. %
Annelida	10 070	5 713	22.68
Nemertea	915	377	38.56
Echinodermata	522	372	54.16
Sipuncula	0	7 706	62.93
Arthropoda	610	9 959	71.57
Chordata	140	1	79.94
Cnidaria	134	26	87.69
Mollusca	177 570	912 910	95.36

Emerald Bank & Western Bank

Phylum	Emerald Bank mean biomass (mg)	Western Bank mean biomass (mg)	Cum. %
Echinodermata	7 192	15 903	16.98
Cnidaria	1 159	3 976	30.36
Mollusca	17 507	266 605	41.23
Brachiopoda	2	2 381	51.80
Annelida	10 076	27 003	62.32
Chordata	442	1 933	70.76
Sipuncula	67	9	78.22
Arthropoda	276	2 278	83.73
Bryozoa	3	55	89.07
Nemertea	234	172	94.38

Sable Island Bank & Western Bank

Phylum	Sable Island Bank mean biomass (mg)	Western Bank mean biomass (mg)	Cum. %
Cnidaria	134	3 976	15.00
Echinodermata	522	15 903	27.98
Brachiopoda	0	2 381	40.60
Annelida	10 070	27 003	51.66
Chordata	140	1 933	60.53
Nemertea	915	172	69.27
Mollusca	177 570	266 605	75.79
Arthropoda	610	2 278	82.28
Bryozoa	0	55	88.67
Porifera	0	39	93.74

Banquereau & Western Bank

Phylum	Banquereau mean biomass (mg)	Western Bank mean biomass (mg)	Cum. %
Echinodermata	372	15 903	20.38
Annelida	5 713	27 003	34.86
Cnidaria	26	3 976	48.54
Brachiopoda	0	2 381	59.85
Chordata	1	1 933	70.25
Sipuncula	7 706	9	76.86
Bryozoa	16	55	82.30
Arthropoda	9 959	2 278	87.24
Porifera	0	39	91.77

The results of the MDS, ANOSIM and SIMPER analyses were very interesting for a couple of reasons. First, samples within a bank clustered relatively tightly (Fig. 2). This

suggests that phylum biomass composition was somewhat conserved across samples on a given bank, indicating that phylum biomass composition may not be useful to detect changes in benthic biodiversity at small localized scales on a given bank. Second, relatively distinct bank communities were distinguished using very coarse taxonomic (i.e., phylum) biomass data. This indicator could prove to be very useful in characterizing and identifying distinct benthic communities on the Eastern Scotian Shelf, as detailed species lists and species-level data are not necessary to indicate the taxonomic uniqueness of each bank or differences at larger spatial scales.

The ability to discriminate banks using very coarse taxonomic data prompts considering why phylum biomass differed so greatly. First, several natural environmental variables could potentially produce large scale differences in benthic biodiversity on the Eastern Scotian Shelf. The combined effects of current speed and direction, food and larval supply of oceanographic currents, depth (a composite of several factors itself), and substrate type and stability could all potentially structure phylum biomass. The banks considered in this study differed greatly in environmental conditions, and these differences could explain a lot of the spatial variation in phylum biomass across the four banks. Taxonomic data at finer levels will help answer this question, because certain taxa may have affinities for specific substrates, currents, food type that largely determine their distributions. As more refined species data become available, benthos could be geo-referenced by identifying sediment-fauna affinities on the Eastern Scotian Shelf. Geo-referencing benthic data will greatly assist to groundtruth predictions about the composition of benthic assemblages under large-scale geographical models.

Indicators of structural species diversity - species heterogeneity

Simpson's and inverse Simpson's indices

Simpson's index λ (Simpson 1949) weights the contribution of species according to their abundance, and represents a "dominance" index:

$$\lambda = \sum_{i=1}^{s} p_i^2$$

where $p_i = n_i / N$

The measure λ is estimated from n_i (the number of individuals of the i^{th} species), and N (the total number of individuals in the sample). λ ranges from 0 to 1, where $\lambda=1$ means that biodiversity is low i.e., all species are represented in equal numbers in each sample. Simpson's index λ is sometimes reciprocated as the inverse Simpson's index $1/\lambda$ (Peet 1974). The smaller the value of $1/\lambda$, the lower the biodiversity in that sample.

For the sake of brevity, only the inverse Simpson's index was reported here Western Bank (Table 11).

Table 11. Inverse Simpson's index within a bank.

Corridor	Sample size	Mean	Standard deviation
B	2	27.526	2.666
E	10	22.186	8.338
G	3	13.282	12.728
I	2	25.499	25.427

Shannon's index

Shannon's index is the most widely used species diversity indicator (Mouillot and Leprêtre 1999). Shannon's index **H′** incorporates the relative abundance of species **p** in a sample with **s** species:

$$H' = -\sum_{i=1}^{i=x} p_i \ln p_i$$

Shannon's index was reported for benthos from Western Bank (Table 12).

Table 12. Shannon's index within a bank.

Corridor	Sample size	Mean	Standard deviation
B	2	3.810	0.016
E	10	3.622	0.421
G	3	3.189	0.842
I	2	3.700	0.656

Pielou's index of evenness

Pielou's evenness index **J′** (Pielou 1975) measures the contribution of each species to the overall sample. In assemblages with high evenness, all species are relatively equally proportioned in the sample. Evenness is measured as:

$$J' = H'_{obs} / H'_{max}$$

H'_{max} is simply the maximum possible diversity if all species were equally abundant (=ln **s**) and H'_{obs} is simply Shannon's Index.

Pielou's evenness index was reported for benthos from Western Bank (Table 13).

Table 13. Pielou's evenness index within a bank.

Corridor	Sample size	Mean	Standard deviation
B	2	0.823	0.019
E	10	0.786	0.087
G	3	0.685	0.177
I	2	0.792	0.101

Like **H′**, **J′** showed significant spatial variation within Western Bank. Shannon's (**H′**) and Pielou's (**J′**) indices are biased when many species are present in the sample i.e., >1000 (Mouillot and Leprêtre 1999) because they are sensitive to changes in rare species. However the reciprocated Simpson's index $1/\lambda$ shows relatively little bias, even when few individuals are present in a sample. At fewer than 25 species, Shannon's index can be estimated with less error than $1/\lambda$. It was not likely that either **H′** or **J′** were biased for estiamtes on Western Bank, as the mean number of species ranged from only 108 to 111 taxa (Table 4).

Taxonomic diversity and distinctness

Warwick and Clarke (1995) described 2 new diversity indices that are both empirically related to Shannon's index **H′**. The hierarchical level of biodiversity appeared to change with perturbation even though species richness and traditional heterogeneity indices like **H′** and **J′** did not change. Taxonomic diversity (Δ) and taxonomic distinctness (Δ^*) measures are both related to **H′**, but have an additional element of taxonomic separation:

$$\Delta = \frac{\Sigma\Sigma_{i<j}\, w_{ij}\, x_i\, x_j + \Sigma_i\, [0.x_i\,(x_i-1)]\,/\,2}{\Sigma\Sigma_{i<j}\, x_i\, x_j + \Sigma\,[x_i\,(x_i-1)]\,/\,2}$$

The index Δ can be thought of as the mean taxonomic distance between any two individuals chosen randomly from the sample, based on the abundance of the ith and jth species (x_i and x_j, respectively) (Clarke and Warwick, 1998). The more taxonomically distinct species **i** is to species **j**, the greater the "distinctness weight (w_{ij})" that is assigned between this species pair. Taxonomic distinctness Δ^* is the ratio described by Δ divided by the value of Δ when all species belong to the same genus, estimated as:

$$\Delta^* = \Sigma w_k f_k / \Sigma f_k$$

where w_k is the distinctness weight over **k** phylogenetic levels, and f_k is the cross-product between all species pairs at the same phylogenetic level.

The measure Δ^* can be applied to biomass, percent cover or binary data. In the latter case, this statistic converges to Δ^+ i.e., the average taxonomic path length between two random individuals (Clarke and Warwick 1998). Note that Δ^* is lowest when all species belong to the same genus, and highest when all taxa belong to completely different phyla. For example, a loss of taxonomic biodiversity at polluted sites was noted when taxonomic distinctness was compared with Δ^* values from more pristine areas (Warwick and Clarke 1998).

These biodiversity measures are independent of sampling intensity, unlike species richness and heterogeneity measures that are affected by the number of observed species. These indices can also be used to compare benthic biodiversity between habitats with little to no degradation, traditionally done using estimates of β-diversity (Warwick and Clarke 1998). In general, highly disturbed benthic assemblages were comprised of more closely related taxa. Warwick and Clarke recognized Δ^* as "by far the most sensitive univariate measure of community structure..."

Taxonomic diversity and distinctness indices were estimated for benthos on Western Bank (Table 14).

Table 14. Mean taxonomic diversity (Δ) and distinctness (Δ*) within a bank.

Corridor	Mean Δ	Mean Δ*
B	81.77	84.54
E	83.81	87.29
G	74.53	86.73
I	82.42	86.23

Both Δ and Δ^* estimates were relatively stable within areas on Western Bank.

Indicators of structural species diversity - indicator taxa

Surrogate measures of species diversity use fewer taxa as estimates to proxy overall diversity. These methods assume that species-rich habitats with many endemic or rare species for indicator groups are indicative of similar trends in other taxa. With respect to the ESSIM initiative, these approaches facilitate the conservation of benthic diversity and the monitoring of ocean activity impacts because they require the examination of survey data from fewer taxa.

Dominant taxa

Species dominance reflects the evenness of species diversity and proportions. Assemblages with low evenness J' are composed of few species but in high proportions. One approach to monitoring benthic biodiversity involves enumerating dominant taxa to determine whether the proportions of dominant fauna or the dominant species themselves are different at various spatial scales. But since preliminary analyses revealed that grab

samples on Western Bank were consistently dominated by the amphipod *Ericthonius fasciatus* and the polychaetes *Thelepus cincinnatus* and *Chone duneri*, the value of using dominant taxa as indicators to detect small scale differences within a bank appeared limited.

Opportunistic species

In addition to environmental variables, the biogeography of benthic organisms can be attributed to species' life history traits (e.g., lifespan, fertility, growth rate, age to maturity). Sanders' (1968) "stability-time hypothesis" categorized life histories of organisms from stable and unstable habitats (Table 15). Species with "equilibrium" traits maximize the competitive ability of that organism with respect to neighbouring fauna by increasing ecological specialization (Dayton and Hessler 1972, Grassle and Sanders 1973). "Opportunistic" traits allow species to rapidly exploit resources, but are not highly specialized.

Table 15. Life histories of organisms from stable and unstable environments (*sensu* Sanders 1968).

Traits of organisms in "predictable" habitats	**Traits of organisms in "disturbed" habitats**
small population size	large population size
large body size	small body size
long lifespan	short lifespan
short-lived or no dispersal stage	long-lived or highly planktonic dispersal stage
low genetic diversity	high genetic diversity
morphologically stable	morphologically variable
endemic and stenotopic distribution	cosmopolitan and eurytopic distribution
rarely hybridize	frequently hybridize
low fecundity	high fecundity
asexually ("clonally") reproductive	sexually reproductive

Grassle and Grassle (1974) provided a simple ranking of several polychaete species based on the degree to which each experienced high mortality. Four of the six taxa they described were found in samples from Western Bank, and these taxa were ranked from most to least opportunistic: *Capitella capitata*, *Polydora* sp., Syllidae and *Mediomastus ambiseta*. This convenient ranking allowed a direct analysis of the sensitivity of using these taxa as indicators of benthic biodiversity to detect differences within a bank (Table 16).

Table 16. Abundance of opportunistic and equilibrium polychaete species on Western Bank.

Capitella capitata

Corridor	Sample size	Mean abundance per grab	Standard deviation
B	2	0.000	0.000
E	10	0.100	0.316
G	3	0.000	0.000
I	2	0.500	0.707

***Polydora* sp.**

Corridor	Sample size	Mean abundance per grab	Standard deviation
B	2	2.500	2.121
E	10	2.000	1.155
G	3	3.667	2.082
I	2	5.000	4.243

Syllidae

Corridor	Sample size	Mean abundance per grab	Standard deviation
B	2	24.500	7.778
E	10	19.800	10.229
G	3	10.333	3.786
I	2	10.500	10.607

Mediomastus ambisetus

Corridor	Sample size	Mean abundance per grab	Standard deviation
B	2	0.000	0.000
E	10	0.100	0.316
G	3	0.333	0.577
I	2	0.000	0.000

Not only was polychaete abundance relatively stable within the fine scale considered here, but the standard deviations were relatively high for all four polychaete taxa, even when sample size was large e.g., in corridor E (Table 16). These problems point to potential difficulties of using these taxa as indicator species. Polychaete abundance could potentially be controlled by highly localized processes operating at very fine scales e.g., levels of sediment bioturbation, food availability, predation.

Indicators of functional diversity – feeding guilds

Feeding guilds are groups of species that exhibit similar feeding strategies and thus contribute to trophic energy transfer in the same manner. Groups can be delineated into categories of feeding preferences. For example, a "macrobenthic predator" is a species that feeds almost exclusively on the macrobenthos. A "surface deposit feeder" is a species that acquires its energy almost entirely from small surficial organisms such as diatoms and protozoans from the sand and mud. It is important to establish the extent to which guild composition is affected by ocean activities because ecosystem development depends on both biomass and productivity (Christensen and Pauly 1993).

Benthic species from Western Bank were grouped into 9 functional feeding guilds: (1) omnivores, (2) macrobenthic predators, (3) filter feeders, (4) suspension feeders, (5) detritivores, (6) subsurface deposit feeders, (7) surface deposit feeders, (8) biogenic film grazers and (9) scavengers. Differences in the abundance of feeding guilds within Western Bank were examined (Fig. 3).

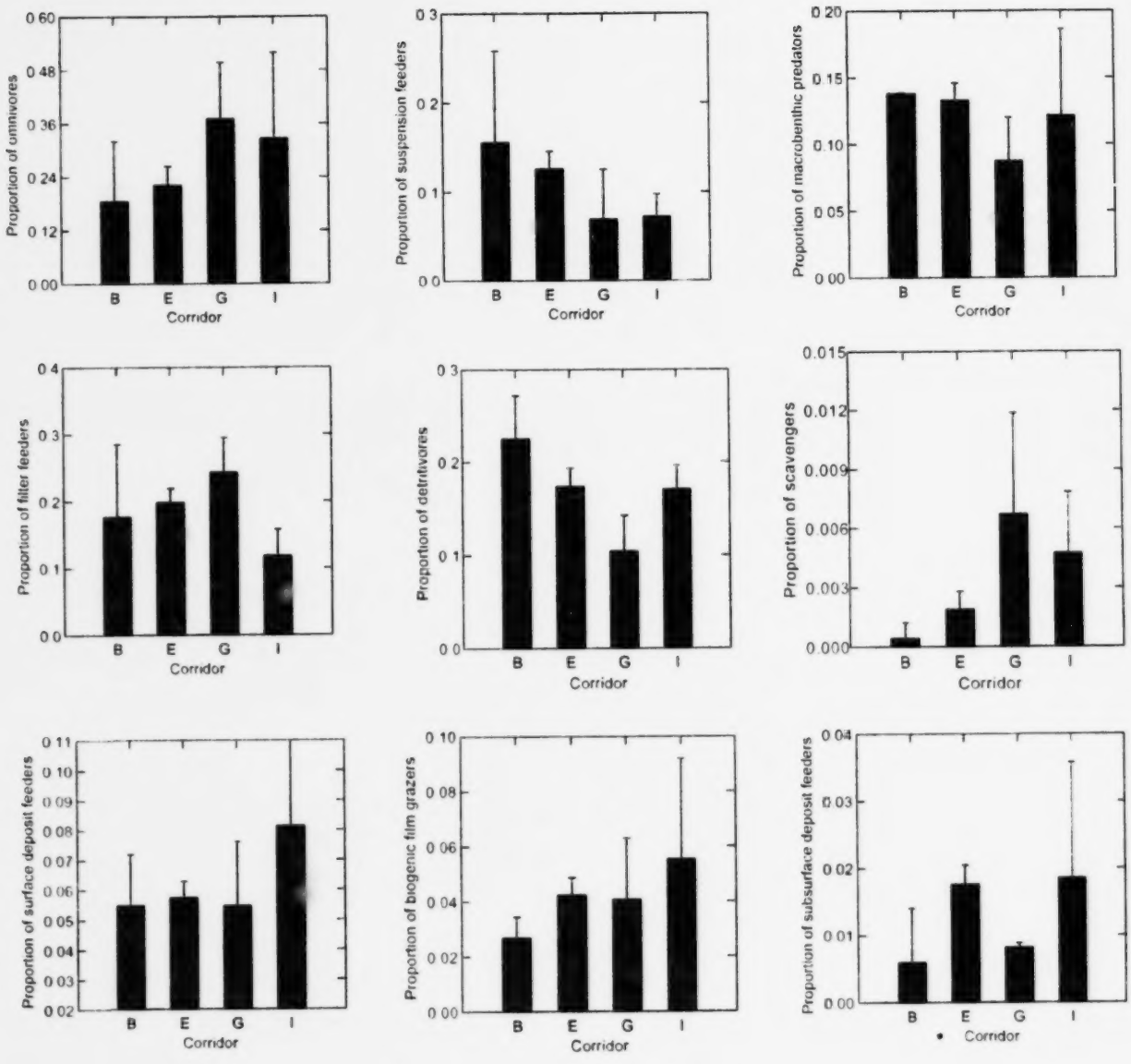

Figure 3. Spatial variation in feeding guilds on Western Bank. Bars represent +/-2 standard errors.

Figure 3 provided a couple of insights into the biodiversity of benthic invertebrate feeding guilds on Western Bank. First, there was considerable spatial variation in the proportion of each guild over the small area sampled on Western Bank. Second, omnivore and filter feeder abundance consistently dominated the communities, while scavengers and subsurface deposit feeders were relatively less abundant.

Indicators of functional diversity – biogenic fauna

Substrates are often limited resources in the marine environments. With respect to ecosystem considerations for the ESSIM area, an additional category of potential indicator of diversity to be considered includes benthic groups that provide habitat to marine organisms including commercially important fish and shellfish. The validity of using such indicators has recently been highlighted as the loss of biogenic structure can significantly decrease marine biodiverity (Thrush et al. 2001).

Long-lived and competitively superior species provide critical habitat for highly diverse epifaunal assemblages, and attract a diverse array of fish and crustaceans. Many benthic taxa on Western Bank form biogenic structures that enhance the physical complexity of epibenthic habitats e.g., sponges, hydroids, anemones, bryozoans, surface-dwelling bivalves, brachipods, crabs and tubiculous (tube-forming) polychaetes. Microhabitat availabilty could be enhanced by these animals so that both ephemeral and longer-lived species can coexist, resulting in substantially higher levels of marine biodiversity.

Benthic fauna were classified into 7 categories based on the way in which they contributed to biogenic structure: (1) sessile and soft-bodied (e.g., some burrowing polychaetes, (2) mobile and soft-bodied (e.g., nemerteans), (3) erect and/or arborescent (e.g., hydroids, bryozoans), (4) sedentary and tubiculous (e.g., some polychaetes, amphipods), (5) mobile and tubiculous (e.g., some amphipods and polychaetes) and (6) sessile hard substrates (e.g., surface-dwelling bivalves) and (7) mobile hard substrates (e.g., gastropods, crabs). The biodiversity of benthic biogenic species was examined using abundance data on Western Bank (Fig. 4).

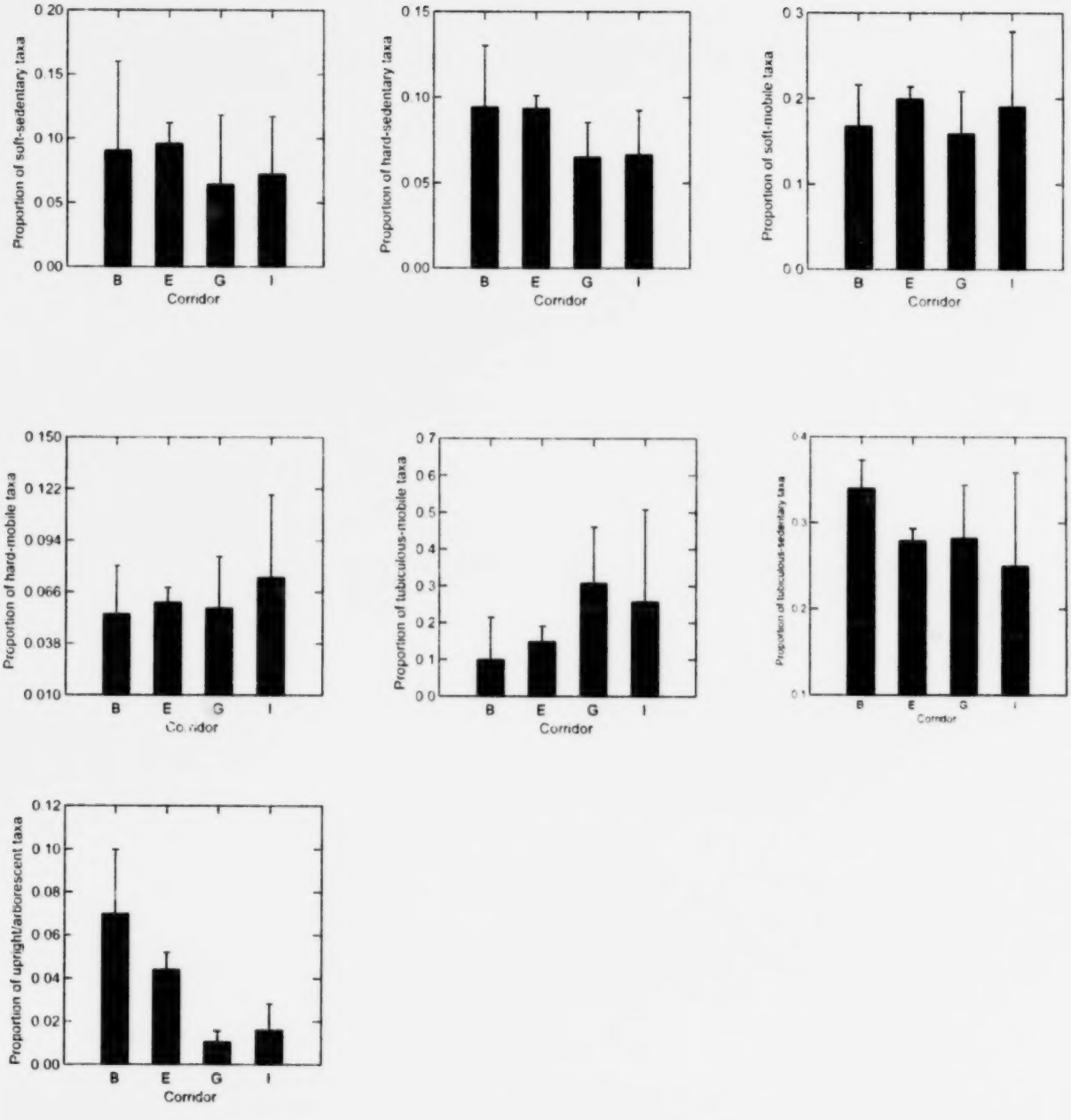

Figure 4. Spatial variation in biogenic fauna on Western Bank. Bars represent +/-2 standard errors.

The consistently high abundance of sedentary tubiculous fauna and hard biogenic substrates suggests that Western Bank could be comprised of highly diverse assemblages of macroinvertebrates, epifaunal organisms and fish associated with biogenic fauna. The relatively stable proportions of these organisms over a small area on Western Bank could reflect the spatial "predictability" of these substrates for colonizing epifauna. Proportions of most other biogenic categories differed at a fine scale on Western Bank, but sedentary tubiculous fauna were consistently the most abundant group.

Benthic colonial organisms greatly contribute to the three-dimensional complexity in marine habitats. Specific attention was paid to these taxa on Western Bank by examining the spatial variation in sponge, bryozoan and hydroid biomass across corridors on Western Bank (Table 17).

Table 17. Biomass of benthic colonial fauna on Western Bank.

Porifera

Corridor	Sample size	Mean biomass (mg)	Standard deviation
B	2	167	199
E	10	2 875	5 246
G	3	6	5
I	2	72	102

Bryozoa

Corridor	Sample size	Mean biomass (mg)	Standard deviation
B	2	105	148
E	10	41	75
G	3	0	0
I	2	0	0

Hydroids

Corridor	Sample size	Mean biomass (mg)	Standard deviation
B	2	4	5
E	10	25	29
G	3	13	22
I	2	0	0

The biomass of colonial organisms (particularly sponges) varied greatly over a fine scale on Western Bank. This points to the potential utility of using colonial organisms to indicate fine-scale changes to benthic biodiversity. The affinities of sessile colonial organisms for relatively stable or cryptic habitats (Jackson 1977) suggests that increased abundance of these taxa could be used as indicators of habitat disturbance. Their distributions may also indicate changes to physical environmental factors, as colonial animals are typically suspension feeders Their abundances may therefore be controlled by

changes in food availability, current flow or epibenthic subtrate availability that permit these species to feed without being smothered.

RECOMMENDATIONS OF BENTHIC BIODIVERSITY INDICATORS

The utility of the various benthic biodiversity indicators described in Part I were summarized in context of several factors (Table 18): their sensitivities to detect differences across various spatial scales, the reliability of their estimated values, and experimental design considerations necessary for their measurements. Justifications are provided below.

Indicators of species richness and heterogeneity (number of species, Margalefs's, Menhinick's, Simpson's, Shannon', Pielou's, taxonomic distinctness and diversity indices)

There was some variation in species richness and most heterogeneity values within and across banks on the Eastern Scotian Shelf. Number of species, Margalef's and Menhinick's were not useful in detecting differences at fine scales (i.e., within a bank). Although these indicies did not consistently detect differences between all 4 banks, large differences in benthic biodiversity were found when comparisons with Western Bank were made, pointing to potentially unique features of this bank. Phylogenetic differences within a bank and across a large scale were detected, but mean biomass estimates had large standard deviations. Taxonomic diversity (Δ) and distinctness (Δ^*) values were stable values on Western Bank. Simpson's index detected fine scale differences but the values were not reliably estimated. As species data become available for the other 3 banks, it would be useful to see whether heterogeneity indicators could be used to detect larger scale shelf-wide differences.

With the exception of phylogenetic differences, all of these univariate richness and heterogeneity indicators required enormous sorting and taxonomic efforts. But these measures frequently detected fine scale and larger scale differences in benthic biodiversity on the Eastern Scotian Shelf, and they are also some of the most commonly reported measures of benthic biodiversity in marine ecosystems. Their discriminating abilities and the potential to compare indicator values across large marine ecosystems should be emphasized to ensure these measures continue to b estimated for benthos in the ESSIM area. Manipulations of existing databases to various levels of taxonomic resolution should be performed to evaluate whether these indicators continue to detect differences at coarser levels (e.g., genus, family, class).

Indicator taxa (dominant taxa and opportunistic species)

The use of "bioindicators" is popularized by the fact that relatively fewer species must be processed than by sorting the entire assemblage in a sample, and that the indicator "opportunistic" or "equilibrium" species responds in a predictable way to human impacts, either by its presence of absence, or by its sheer abundance or biomass in the sample. In general, indicator taxa are not recommended for use as management tools to help address ecosystem objectives for benthos on the Eastern Scotian Shelf. Many taxa are quite small, and must all either be counted, sorted and weighed separately to detect

differences between samples. Furthermore, the high standard deviations associated with their estimation suggests that estimate means are unreliable.

Much of this spatial variability in the distribution of these species could be associated with natural environmental factors, opportunistic life cycles and morphology. These indicators are impractical to use to address ecosystem considerations for the ESSIM area, given any sampling protocol as effects of natural processes may not be separable from the effects of human ocean activities on benthic biodiversity.

Species dominance could reflect naturally patchy distributions of benthos. Benthic organisms exhibit clumped distributions for several reasons. They may exhibit gregarious larval settlement, organisms may clump together for increased defence from predation or being dislodged and swept away by currents, they may clump temporarily during reproductive periods, or they may aggregate during opportunistic feeding periods. Thus, the domination of a sample by a few species could reflect several natural processes as well as potential human ocean activities.

The cons of using opportunistic taxa as indicator species are similar to those using dominant indicator species. Opportunistic taxa rapidly exploit resources, and are quickly replaced by longer lived and competitively superior species. A sample that is dominated by opportunistic taxa may simply reflect a small scale temporary process that induced the colonization of that area by the species in question. For example, a dead or dying animal on the sea floor may induce immediate exploitation of the area by predatory crabs, sea stars, amphipods and annelids. The practial use of opportunistic taxa as indicators of biodiversity on Western Bank appears to be limited. In the case of polychaetes, the opportunistic indicator species used by Grassle and Grassle (1974) such as *Capitella capitata* have the ability to turn over (i.e., replace) their populations in a matter of 48 hours. Determining whether the presence of this species in samples reflects changes induced by the impact of human ocean activities or by natural processes becomes very difficult without first knowing the spatial and temporal scales of the distribution of *C. capitata* patches. More recently, molecular, reproductive and ecological evidence revealed that *C. capitata* is probably a "complex" of several genetically distinct species with very different life histories (Knowlton 2000). Therefore, using opportunistic taxa is also troublesome because these fauna can diverge quite rapidly into distinct species that are virtually indistinguishable in a sample collected at one point in time.

Indicators of functional biodiversity (feeding guilds and biogenic structures)

Feeding guilds

Guilds are popular tools to describe ecosystem structure because their composition implies much about ecosystem function (e.g., primary productivitiy, biomass turnover, respiration). For example, marine ecosystems stressed by pollution may be heavily dominated by primary producers, with few grazers and large predators. Recent physical sea floor disturbance caused by bottom-trawling may inflicted mortality to much of the benthos so assemblages are, at least temporarily, dominated by scavengers, predators and detritivores.

There were moderate levels of natural spatial variation in feeding guild composition on Western Bank. Omnivores and filter feeders were generally the most abundant taxa. Scavengers, deposit feeders and biogenic film grazers showed slight differences in percent contributions to benthic feeding guilds within a bank.

Small scale variations in feeding guild composition could be produced by several natural processes. Opportunistic feeding periods could have caused patchiness for highly mobile scavenging species. Deposit feeders may have been highly abundant on isolated patches of mud and sand with abundant sources of diatoms and organic sediment. Biogenic film grazers may likewise have been attracted to these same patches.

Spatial variation in feeding guild composition could also have reflected how feeding guilds were originally assigned to benthic taxa. There appears to be no standard classification scheme for classifying benthos into feeding guilds. The nine groups assigned here were assumed to be biologically meaningful. Benthos were assumed to discriminate between sources of food, size of food particles, and the means of obtaining food. However it was not known to what extent benthos use these factors to discriminate what to eat and when, so categories such as "specialized" versus "generalist" were not included.

Using feeding guild composition as an indicator of benthic biodiversity is complicated by the fact that feeding affinities are unknown for many benthic marine animals, particularly the amphipods and polychaetes. Feeding behaviours are largely unknown under natural conditions, but are necessary to know as laboratory observations are often highly unnatural (Fauchald and James 1979). Therefore, many of the taxa may actually be omnivores and not predators, or they may scavenge under laboratory settings but feed exclusively on detritus in the ocean. Before feeding guilds can be considered for use as indicators for management tools, more primary research must be done to resolve feeding behaviours of these species.

Feeding guilds would be very useful management tools to help monitor benthic biodiversity. Large shifts in these guilds from their normally "robust" compositions (Jennings et al. 2001) would almost certainly reflect shifts in the functioning of a given

area, which is an additional objective for management plans to address for marine environments. But the moderately high standard errors associated with each feeding guild measure across all corridors on a bank suggest that estimate means are unreliable. Furthermore, the lack of primary research into feeding guild classification makes this indicator impractical as the assignment of species to these categories cannot be accurately done at this point in time for most of the benthos on the Eastern Scotian Shelf.

Biogenic structures

The biogenic complexity of a habitat can be measured many ways, and should probably be done using several methods including video to first assess bottom topography or rugosity generated by living organisms and by the classification of organisms by their morphology and spatial or temporal predictability (i.e., "mobility") on the sea floor. Some fauna are highly susceptible to certain human ocean activities such as bottom trawling e.g., benthic colonial organisms such as sponges, bryozoans and hydroids (e.g., Van Dolah et al. 1987, Collie et al. 1997, Koslow et al. 2001). Both video and grab samples were obtained simultaneously during DFO mobile gear impact experiments, and these data are now accessible to begin assessing habitat complexity and the effects of this human ocean activity. The use of biogenic organisms as indicator taxa must be investigated further because biogenic fauna can contribute much to commercial fish and shellfish production and to enhancing overall biodiversity levels (Thrush et al. 2001). Biogenic faunal composition also requires much less taxonomic effort than richness and heterogeneity measures, and can even be estimated using video instead of grabs that would facilitate sampling larger areas.

A potential problem with using habitat complexity as an indicator of biodiversity is that the classification of species into morphological and mobility categories can be somewhat arbitrary. For example, the current classification scheme produced 9 categories that may or may not be biologically relevant. Some species of fish, shellfish and other organisms that use biogenic animals as habitats may not distinguish a sessile hard-surface species from a sessile tubiculous species, while this difference may be important to other species. Further research could be done to examine what categories are biologically relevant and the extent to which species discriminate between such categories.

Assuming that fauna were classified into biologically relevant categories, there was a moderate amount of spatial variation in biogenic complexity across corridors on Western Bank, particularly in the percent contributions of mobile tubiculous and erect/arborescent fauna. But the moderately high standard errors associated with biogenic complexity values on Western Bank suggest that estimate means may not be reliably obtained. The fine scale variation in mobile tubiculous and erect/arborescent fauna could reflect true spatial variability in the distribution of these biogenic groups across the sea floor due to localized physical habitat characteristics such as sand mounds, depressions, boulders or current velocity variations. Alternatively, or possibly in conjunction with localized differences in physico-chemical characteristics of the local environment, fine scale variability may be due to biological factors such as gregarious settlement of larvae or

to species temporarily aggregating during opportunistic feeding or reproductive activities in one area but not another. Spatial variation could also have reflected inadequate sampling of taxa that contributed to these biogenic groups.

Using habitat complexity to indicate changes in benthic biodiversity may only be applicable to specific types of human ocean activities. For example, the effects of mobile bottom fishing gear on the abundance or proportion of each species in a biogenic category may not be the same for the effects of other human ocean activities such as marine pollution or ballast water exchange. The functional role of biogenic complexity reflected in marine environments is becoming an important research topic as it could help answer the question of what controls fisheries production and benthic biodiversity. Due to the high probability that morphological and mobility categories may only serve to detect specific impacts, this type of indicator could be specifically recommended for studies that evaluate the effects of specific human ocean activities where the physical bottom habitat is potentially modified, e.g., the use of mobile fishing gear (Schwinghamer et al. 1998).

The fine scale spatial variability in this indicator also points to using biogenic complexity as an indicator to assist in identifying geographic areas with high levels of biodiversity that are potential candidates for marine protected area status. For example, if several banks were to be compared, an area with the highest variability in these indicators across replicate samples could indicate more diverse ecosystems, habitats, communities, populations, or patches of species given a specified area, gear and sampling protocol that had been standardized across the banks. The standardization itself is problematic however, in that great effort and cost must be taken to ensure samples are taken in the same way across all sites. Examining the variation in samples has a strong statistical basis in that much can be learned about the randomness, distribution patterns and clumped tendencies of marine benthos by examining such measures as coefficients of variation, standard errors and standard deviations of the means. Future research should examine spatial variation in biogenic complexity to determine if trends are real or reflect sampling inadequacies.

Table 18. Summary of recommendations for the use of benthic biodiversity indicators for the Eastern Scotian Shelf (✔ = good, ✘=poor, ?=not evaluated).

Indicator	Bank-wide differences	Shelf-wide differences	Reliability of estimated values	Experimental considerations
Number of species	✘	✔	✔	✘
Margalef's index	✘	✔	✔	✘
Menhinick's index	✘	✔	✔	✘
Phylogenetic structure	✔	✔	✘	✔
Simpson's index	✔	?	✘	✘
Shannon's index	✘	?	✔	✘
Pielou's index	✘	?	✔	✘
Taxonomic diversity and distinctness	✘	?	✔	✘
Dominant taxa	✘	?	?	✘
Opportunistic taxa	✔	?	✘	✔
Feeding guilds	✔	?	✘	✘
Biogenic fauna	✔	?	✘	✔

INDICATORS OF GENETIC BIODIVERSITY

Genetic biodiversity in the sea

Very little is known about how human ocean activities affect ecological processes such as recruitment, fecundity, survival or growth that modify evolutionary processes driven by genetic biodiversity in most benthic organisms on the Eastern Scotian Shelf. Most genetic research has been done on commercially important fish and shellfish species e.g., sea scallop *Placopecten magellanicus* (Patwary et al. 1994, Pogson and Zouros 1994, Gjetvaj et al. 1997, Herbinger et al. 1998) and American lobster *Homarus americanus* (Tam and Kornfield 1996, Harding et al. 1997).

"Short-term" ecological processes have direct impacts on the "longer-term" evolution of each species. For example, reduced recruitment, higher mortality and reduced fecundity may limit the amount of genetic diversity in a population by reducing dispersal and gene flow, producing populations with little genetic variation left (Van Dover et al. 2002). Subsequent disturbances may then permanently remove all the remaining individuals.

Genetic analyses would be very useful tools to measure how ocean activities affect the biodiversity of benthic invertebrates on the Eastern Scotian Shelf. Genetics help define species boundaries through measures of genetic differentiation (Knowlton 2000). These tools allow the estimation of the contribution of sexual versus asexual reproduction in various fauna e.g., anemones (Shick et al. 1979, Ayre 1984, Hoffman 1986, 1987), and corals (Ayre and Willis 1988, Coffroth et al. 1992, Hunter 1993, Brazeau and Harvell 1994, McFadden 1999, Barki et al. 2000). Genetic analyses also allow dispersal capabilities and gene flow to be estimated to help identify species ranges, barriers to dispersal and ultimately patterns in species evolution and biogeography (Van Dover et al. 2002).

What predictions could be made about how human ocean activities affect genetic biodiversity on the Eastern Scotian Shelf? Sanders (1968) predicted that more "stable" environments are composed of genetically undiverse populations. In unstable habitats, a genotype that was selected under previous conditions may no longer be successful, so it is adaptive for an individual to liberate many sexually produced offspring with high genetic variability to ensure that some individuals in the population will possess characters that are suited to new conditions (Williams 1975).

There is some experimental genetic evidence to corroborate Sanders' prediction. Ayre (1984) measured genetic diversity of the sea anemone *Actinia tenebrosa* on subtropical rocky shores. Unstable boulder shores were comprised of genetically more diverse individuals than more stable shores. Hunter (1993) measured genetic diversity of the scleractinian coral *Porites compressa* from Hawaiian reefs and concluded that genetic diversity was lowest on reefs with the lowest levels of storm, anchor and fishing disturbances. Tissue grafts have also been used to model recovery of staghorn coral

Acropora cervicornis populations following disturbance (Neigel and Avise 1983). Low genetic diversity was correlated with high habitat stability and low levels of sexual recruitment into local populations in this species.

Creasey and Rogers (1999) reviewed genetic biodiversity of organisms from deep-sea ecosystems, historically assumed to be "stable" environments. Contrary with Sanders' prediction, Creasey and Rogers found that many species exhibited high genetic biodiversity, so the relationship between genetic biodiversity and habitat stability is not at all straightforward.

High genetic biodiversity in stable habitats can be explained several ways. First, "stable" habitats may not be undisturbed at the scale of a benthic invertebrate. Shelf and deep-sea ecosystems are usually buffered by waves and seasonal variations in temperature and salinity, but chronic disturbances by fast bottom currents and the extent to which substrate and food availability are predictable in space and time make such habitats "unstable" to benthic organisms. Second, habitat availability may be limited or patchily distributed. A lack of gene flow between fragmented populations could drive the genetic isolation of proximately located conspecifics, resulting in complexes of cryptic "sibling species" with varying degrees of reproductive, ecological and genetic isolation (Knowlton 2000). Whether larval recruitment is a limiting factor in these ecosystems must also be determined to help explain observed levels of genetic biodiversity as chronic and intense habitat fragmentation intensifies the importance of successful recruitment (Lasker and Coffroth 1999). Third, larval biology may dictate levels of genetic biodiversity. Invertebrates with high dispersal abilities can still exhibit distinct genetic boundaries between populations (Burton 1983, Palumbi 1994, Degnan and Lavin 1995). In contrast, species with restricted dispersal mechanisms ("philopatric" taxa) can still exhibit genetically diverse assemblages due to passive dispersal mechanisms such as rafting on floating macroalgae (Jackson 1986).

Predictions about the effects of human ocean activities on benthic genetic biodiversity are further complicated when one considers the biology of clonal species i.e., those taxa with the ability to reproduce sexually as well as asexually (e.g., by budding, fission, fragmentation). Clonal organisms are distinguished from aclonal fauna by their indeterminate lifespans and abilities to reproduce without syngamy and recombination in their life cycles, except in rare cases. Growth and propagation are achieved through iterated self-replication that repeatedly expresses particular genotypes. Extensive asexual reproduction can result in very high biomass and dense monocultures of a single genotype, exposing it to a diversity of environments and selective forces (Harper 1985).

The alternation of reproductive strategies in clonal organisms, the lack of long-lived dispersal phases in many species and the potentially infinite genet size in clonal fauna have consequences for gene flow between populations (Jackson 1985, Palumbi 1994). For example, some corals, hydroids and bryozoans exhibit extreme philopatry and highly clonal existences, both which may limit gene flow between populations, promoting inbreeding and introducing genetic drift. Ocean activities that damage organisms, increase

pollution or sedimentation levels can potentially limit sexual reproduction and subsequent larval dispersal, and are thus highly likely to reduce gene flow between populations.

Many clonal species release vegetatively derived but genetically identical propagules that disperse as far as sexually derived larvae (Jackson 1985, 1986). Thus, it may be possible for these organisms to maintain genetic "connectedness" with fragmented populations. Fragmentation could be an important life history trait of many clonal organisms on the Eastern Scotian Shelf e.g., sponges, anemones, corals and bryozoans. This process generally avoids the energy expenditure of sexual reproduction, while increasing the chances that propagules find new substrate, particularly larger fragments that exhibit higher survivorship than smaller ones (Highsmith 1982). Adaptive fragmentation may explain reports of asexual reproduction during recolonization and recovery events in warm-water corals (Hughes and Jackson 1985, Van Veghel and Kahmann 1994) and zoanthids (Karlson 1986). Clonality, long generation time and low fecundity often correlate with environmental stability; when sexual reproduction does occur, it occurs philopatrically to ensure genetically related planulae are retained near parental assemblages to maximize their probability of survival (Jackson 1985).

Concepts in genetic biodiversity

The measurement of genetic biodiversity may be considered the smallest scale of biodiversity for which estimates of the natural variability in biodiversity and the effectiveness of management plans for marine areas can be obtained. The measurement of genetic biodiversity should be considered highly relevant to initiatives that address the conservation of marine biodiversity at higher hierarchical levels. For example, even accurate estimates of species richness depend on the rapidly growing field of molecular technology to deliver genetic evidence for the existence of several closely related "sibling species" that may currently be considered only one species (Knowlton 2000). The amount of genetic biodiversity also provides molecular clues to processes operating at larger scales e.g., levels of connectivity between fragmented marine habitats, the degree of population reduction due to disturbances, and the potential for population recovery from and adaptation to environmental perturbations.

"Genetic biodiversity" broadly encompasses several concepts such as the genetic variability within an individual (i.e., levels of homozygosity and heterozygosity at particular positions on a DNA molecule or "locus"), the amount of genetic variation between individuals ("polymorphisms") and the number of distinct genotypes present in an assemblage. The measurement of all three concepts in genetic biodiversity yields an estimation of overall population genetic "structure".

Several natural mechanisms create and maintain variability in the genetic structure of benthic marine invertebrate populations. Each concept under the umbrella of genetic biodiversity were considered here and commonly used indicators of genetic biodiversity were reported.

Origins and maintenance of genetic biodiversity

Recurrent mutations in parental DNA can be passed on to offspring and the polymorphisms maintained by selection if they confer some selective advantage. They can also be eliminated if they have deleterious effects on the fitness of either the parent or offspring, or they can be maintained if they are not under selective pressure (Ridley 1996).

There are several important mechanisms for the maintenance of polymorphic loci in benthic marine invertebrates and these are broadly classified as either being under the control of the organism itself, or controlled by ecological processes.

Mechanisms that operate at the level of the organism

"Genic" (i.e., at the level of a locus) and "cytogenetic" (i.e., at the level of the cell) control and the concept of "heterosis" (i.e., selective advantage of a heterozygous loci) maintain polymorphic loci by affecting the expression of traits under genetic control (i.e., the phenotype of the organism), the persistence of unfavoured alleles at a loci, and the selective superiority of heterozygotic loci (Ridley 1996).

Genic maintenance of polymorphism arises under several conditions. In the first case, otherwise deleterious alleles persist because they are recessive and possible not under natural selection. Under a second condition, interactions between loci reduce the phenotypic effect of the deleterious allele or locus, a concept known as "epistasis". Under a third condition, polymorphisms are maintained because some alleles are simply not fully expressed phenotypically (limited "expressivity") or because members of the population may not express the phenotype at all (limited "penetrance").

Cytogenetic maintenance of polymorphism arises because loci can be physically linked and often inherited together (a phenomenon known as "linkage disequilibrium"), or because alleles are do not assort randomly during meiosis so that heterozygotes are maintained in the population (a process known as "meiotic drive").

Heterosis is the concept that heterozygotes confer a selective advantage over individuals that are homozygous at certain loci. This could occur because loci that code for enzymes have greater activity or are functional over a greater range of environmental conditions as they possess both forms (alleles) of an enzyme. Homozygous loci may have deleterious effects, so having both allele forms is favoured under natural selection.

Mechanisms that are controlled by ecological processes

Polymorphisms are also maintained by spatial and temporal variation in selective pressures. This results in certain alleles being selected for in a given space and time. Selection may vary according to the ontogeny (the life history), seasonal or climatic

changes experienced by an individual, or during episodes of great disturbance such as cyclones, or geological events such as glaciation. Polymorphisms can also be maintained due to the somewhat inefficiency of selection at times, so that not all individuals with a deleterious allele are eliminated, and not all individuals with advantageous alleles are selected to survive and reproduce. Random, negative assortive mating can also produce polymorphisms because this maintains more heterozygotes in the population. Polymorphisms are also maintained in the case of frequency-dependent or density-dependent selection where rare alleles are favoured over more abundant forms (Ridley 1996) e.g., in predator-parasite interactions, or on highly crowded substrates where rare alleles are selected for because they confer some kind of resistance to disease or to competition for space.

Genotypic diversity in benthic marine invertebrates

The number of genetically distinct individuals in a population is controlled by several factors including genetic drift, effective population size, reproductive success, recruitment, and sex ratio. Disturbances to the marine environment that impair any of these parameters reduce the number of genetically distinct individuals, leading to closely related individuals mating with each other and consequently reduced heterozygosity i.e., "inbreeding depression". Assemblages of closely related individuals may not contain sufficient genetic biodiversity to adapt them to future perturbations. For example, disturbances that fragment marine environments can drive the separation of populations (the "genetic connectivity") so that these assemblages evolve differently and result in reproductively isolated populations even after the disturbances have subsided.

Research efforts to evaluate the impacts of mobile bottom fishing gear on the Eastern Scotian Shelf have recently highlighted the susceptibility of sessile emergent fauna to this human ocean activity, and points to the potential for increased fragmentation of benthic populations. Population fragmentation and loss of genetic biodiversity in these organisms is of considerable concern as these epibenthic organisms form complex biogenic structures that attract fish, molluscs, and a diverse assemblage of associated epifauna (Van Dolah et al. 1987, Hutchings 1990, Gili and Hughes 1995, Thrush et al. 1995, Tupper and Boutilier 1995, Auster et al. 1996, Collie et al. 1997, Magee et al. 2000, Henry 2001). The discovery of pharmaceutically useful bioactive products from sponges, bryozoans and corals also prompts the need to study clonal taxa as the production of these compounds is to a variable degree under genetic control (Hay 1996, Hay and Fenical 1996, Davidson and Haygood 1999).

Commonly used indicators of genetic biodiversity

Several indicators can be used to measure genetic biodiversity, depending on whether the estimation of heterozygosity in a population, polymorphisms across populations, or the number of genetically distinct individuals is required. A review of molecular techniques and measures of genetic biodiversity was provided by Silva and

Russo (2000). Common indicators were described here for future reporting of benthic genetic biodiversity estimates obtained from the Eastern Scotian Shelf.

Indicators of heterozygosity

Nei's Index of genetic diversity (Nei 1973) is the most frequently used index of heterozygosity ("**H**") (Ridley 1996). It is based on the proportion of heterozygotes "**p**" in an assemblage:

$$H = 1 - \sum p^2$$

A slight variation on this index is derived from Shannon's index in ecology (Lewontin and Hubby 1966):

$$H' = - \sum p \ln p$$

As both **H** and **H′** depend on the frequencies of the most abundant alleles (as **H′** does when one considers species), very rare alleles contribute very little to the final value.

The degree of inbreeding measures the amount of heterozygotes missing under the expectation that the proportion of heterozygotes should occur predictably i.e., under assumptions stated by the Hardy-Weinberg equilibrium theory. The index "**F**" (for fixation of an allele) is the ratio of the number of heterozygotes expected (H_{exp}) and those observed (H_{obs}) from a random sample in a population (Wright 1965, Weir and Cockerman 1984):

$$F = (H_{exp} - H_{obs}) / H_{exp}$$

Indicators that measure polymorphisms across populations

"Genetic differentiation" refers to the amount of polymorphisms across populations, and measures the mean genetic distance among all pairwise combinations of populations (Kremer et al. 1998). The most commonly reported index of genetic differentiation is Nei's genetic distance measure D_s (Nei 1987), based on a measure of genetic identity "**I**" that considers the summed mean of locus **i** from J_{xy}, J_x and J_y in 2 populations, **x** and **y**:

$$J_{xy} = \sum x_i y_i ; \; J_x = \sum x_i^2 ; \; J_y = \sum y_i^2$$

and

$$I = J_{xy} / \sqrt{J_x J_y}$$

where

$$D_s = - \ln I$$

A second commonly reported index of differentiation is $D_{1,2}$ and is based on the proportion of shared alleles across two populations, 1 and 2 ($P_{1,2}$) (Bowcock et al. 1994):

$$D_{1,2} = 1 - P_{1,2}$$

The measurement of the number of genetically distinct individuals

With the exception of clonal organisms, measuring the number of genetically distinct individuals in an assemblage is as informative as measuring the number of species in a sample, and suffers from the same drawback as species richness measures as it is highly sensitive to sample size. It is expected that all individuals sampled will be a different genotype, although depending on the genetic technique being used, this may be more readily apparent e g., the use of fewer microsatellite loci versus to look for differences can require the use of many enzyme loci to detect the same number of distinct genotypes.

Clonal organisms cannot be excluded as they may potentially comprise much of the structural (e.g., species biodiversity) and functional (e.g., feeding guilds and habitat complexity) components of benthic habitats on the Eastern Scotian Shelf. To measure the extent of genetic biodiversity in clonal organisms, the number of physically separate individuals/colonies (="ramets") and the estimation of the number of genotypes (= genets) must be measured. In a strictly sexually reproducing assemblage, the number of ramets "**R**" = the number of genets "**G**" so that:

$$R/G = 1$$

In an assemblage where asexual reproduction i.e., cloning is highly prolific, one would expect a situation where there are many more ramets for every genet so that:

$$R/G \gg 1$$

In practice, the estimation of genotypic diversity (or "**d**") requires the measurement of the number of different genotypes per number of individuals sampled so that **d** varies between 0 (purely asexual) and 1 (purely sexual) (Hoffman 1986). The most commonly used indicator to measure genotypic diversity is expressed by the ratio:

$$d = G_O / G_E$$

G_O is the observed number of genotypes described by the equation:

$$G_O = 1/\Sigma p_i^2$$

where p_i is the frequency of the ith genotype in a population. G_E is the number of genotypes expected under purely sexual reproduction, described by the equation:

$$G_E = 1/(D+P/N)$$

where **D** is the sum of all p_i^2 and **P** is the sum of all p_i in a sample of **N** individuals (see Stoddart and Taylor 1988 for derivations).

High reliability of the genetic biodiversity estimate is difficult to achieve since sample size will be correlated to G_O / G_E. This can partially be resolved by sampling the same number of ramets in each population. The accuracy of the measurement necessarily increases with sample size as more of the population contributes to the overall estimate. This must be balanced by the practicality of sampling as many ramets as possible in a population.

MANAGEMENT IMPLICATIONS

Recommended indicators

Many of the indicators described within this report are commonly used in both terrestrial and marine biodiversity studies. These indicators and several other, less commonly used measures were examined to determine their potential utility in detecting small and large-scale differences in benthic biodiversity in the ESSIM area. It is recommended that a combination of these indicators be used to monitor and maintain benthic biodiversity in the ESSIM area as several measures provide greater insight into variation in biodiversity estimates than a single index (Levin et al. 2001).

The enormous taxonomic effort required to estimate potentially very useful richness and heterogeneity indicators points to the need for comparative studies that examine whether coarse taxonomic information can replace species-level data to measure these indicators.

Functional indices also have the potential to serve as biodiversity indicators, particularly the classification of benthos into biogenic groups. Various forms of this indicator are becoming increasingly common in studies that assess effects of human ocean activities that impact the sea floor. This indicator is relatively easy to measure particularly if video sampling can be supplied, and is also directly relevant to commercial fish and shellfish production, and to the biodiversity of marine species in general.

The past 10 years have been marked by directed scientific effort into describing benthic communities on the Eastern Scotian Shelf (see recent syntheses on the Gully in Gordon and Fenton (2002) and the Scotian Shelf in general by Stewart et al. 2001) that will aid management plans to conserve and protect benthic biodiversity in this area (O'Boyle 2000). Since the initiation of the current study, benthic databases have expanded and now contain highly detailed information on the benthos from several areas on the Eastern Scotian Shelf obtained by video, still photographs, grabs, sleds and suction deviese during various studies. Complete syntheses of this information is expected to yield a wealth of information regarding benthic biodiversity on the Eastern Scotian Shelf that would be highly relevant to management needs for this region.

Is Western Bank unique?

This report provided some new knowledge of benthic communities on Western Bank that may assist in establishing a large marine closure area to conserve and protect benthic biodiversity on the Eastern Scotian Shelf. Western Bank consistently had higher species richness. The high biomass of echinoderms and cnidarians on Western Bank helps distinguish this bank from the others, and is reminiscent of the high biomass of echinoderms observed on the Grand Banks (Gordon et al. 2002). Factors that contribute to assemblages of echinoderms and cnidarians are probably related to substrate-fauna

affinities, and the importance of such associations should be evaluated in future research efforts as more complete species data are available to better understand these affinities.

Indicators of genetic biodiversity

Very little is known about levels of benthic genetic biodiversity on the Eastern Scotian Shelf. The estimation of any genetic biodiversity indicator at this point will be financially costly and require great investments of time and scientific effort. Yet these estimates can reflect ecological and evolutionary processes that structure levels of biodiversity e.g., recruitment, fragmentation, population sizes. Until genetic studies become routinely financially and technically feasible, molecular projects on non-commercial benthos should probably be opportunistic (e.g., as ideal projects for students), limited to species at risk of becoming extinct/locally extirpated, or to those that constitute biogenic habitat for fish and other marine species.

SUMMARY

This study provided preliminary evidence for the utility of richness, heterogeneity, phylogenetic and biogenic complexity indicators to detect differences at various spatial scales on the Eastern Scotian Shelf. With the growing availability of complete DFO benthic databases, it should become increasingly easier to evaluate the utility of richness and heterogeneity indicators at coarse taxonomic levels. If the amount of taxonomic effort can be decreased without impairing the discriminating abilities of the indicators, then these measures should serve as excellent tools to help monitor and maintain benthic biodiversity on the Eastern Scotian Shelf. Coarse taxonomic information was sufficient to discriminate phylogenetic differences across banks, and points to the need for increased information on substrate-fauna affinities to understand and predict spatial patterns in benthic biodiversity. The consistently high levels of biodiversity and the potential uniqueness of Western Bank should be examined further to identify factors that structure benthic biodiversity in this area. Research into benthic mapping as it relates to the distribution of biogenic fauna should continue, and the utility of habitat complexity indicators should be addressed given the role of biogenic fauna as fish habitat and as structure for associated fauna. Video should be combined with grab sample analyses to measure biogenic complexity over larger spatial scales. Efforts should continue to correlate the distribution of various biogenic categories to fish habitat and high levels of benthic biodiversity measured in other ways. Until genetic studies become more feasible, it is perhaps recommended that such projects be limited to opportunistic availability of students, to species at risk or those that enhance marine biodiversity in general.

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APPENDIX I. STATION DATA FOR BENTHIC SAMPLES ON THE EASTERN SCOTIAN SHELF

Bank	Year	Vessel	Cruise	Gear Type	Station	Latitude	Longitude	Depth (m)
Banquereau	1998	Hudson	H98-015	0.5m² grab	wa06g1	44.437552	-57.891258	69
Banquereau	1998	Hudson	H98-015	0.5m² grab	wa09g1	44.438082	-57.889723	70
Banquereau	1998	Hudson	H98-015	0.5m² grab	wb02g1	44.436794	-57.893154	69
Banquereau	1998	Hudson	H98-015	0.5m² grab	wb07g1	44.436827	-57.890529	70
Banquereau	1998	Hudson	H98-015	0.5m² grab	wd05g1	44.435833	-57.891303	70
Banquereau	1998	Hudson	H98-015	0.5m² grab	wd08g1	44.435897	-57.889864	70
Banquereau	1998	Hudson	H98-015	0.5m² grab	wi06g1	44.423854	-57.89199	76
Banquereau	1998	Hudson	H98-015	0.5m² grab	wi09g1	44.423911	-57.889794	75
Banquereau	1998	Hudson	H98-015	0.5m² grab	wj02g1	44.420176	-57.894232	78
Banquereau	1998	Hudson	H98-015	0.5m² grab	wj04g1	44.420532	-57.892442	79
Banquereau	1998	Hudson	H98-015	0.5m² grab	xf03g1	44.430665	-57.893978	74
Banquereau	1998	Hudson	H98-015	0.5m² grab	xf06g1	44.430669	-57.892188	75
Banquereau	1998	Hudson	H98-015	0.5m² grab	xf09g1	44.430918	-57.889936	76
Banquereau	1998	Hudson	H98-015	0.5m² grab	xf10g1	44.430729	-57.88964	76
Banquereau	1998	Hudson	H98-015	0.5m² grab	xg02g1	44.430096	-57.894732	75
Banquereau	1998	Hudson	H98-015	0.5m² grab	xg09g1	44.430315	-57.889684	76
Banquereau	1998	Hudson	H98-015	0.5m² grab	xg10g1	44.430396	-57.88916	76
Banquereau	1998	Hudson	H98-015	0.5m² grab	xh01g1	44.429677	-57.895249	75
Banquereau	1998	Hudson	H98-015	0.5m² grab	xh06g1	44.429719	-57.892004	76
Banquereau	1998	Hudson	H98-015	0.5m² grab	xh10g1			76
Banquereau	1998	Hudson	H98-015	0.5m² grab	yc05g1	44.436065	-57.904284	67
Banquereau	1998	Hudson	H98-015	0.5m² grab	yc08g1	44.435843	-57.902463	69
Banquereau	1998	Hudson	H98-015	0.5m² grab	yd01g1	44.435622	-57.906893	72
Banquereau	1998	Hudson	H98-015	0.5m² grab	yd06g1	44.435808	-57.903774	67
Banquereau	1998	Hudson	H98-015	0.5m² grab	yd08g1	44.435513	-57.902384	70
Banquereau	1998	Hudson	H98-015	0.5m² grab	ye03g1	44.434677	-57.905508	68
Banquereau	1998	Hudson	H98-015	0.5m² grab	ye05g1	44.435407	-57.904392	68
Banquereau	1998	Hudson	H98-015	0.5m² grab	ye06g1	44.434928	-57.903556	69
Banquereau	1998	Hudson	H98-015	0.5m² grab	ye07g1	44.434985	-57.902962	69
Banquereau	1998	Hudson	H98-015	0.5m² grab	ye10g1	44.434921	-57.901166	70
Sable Island	1996	Parizeau	P96-009	0.5m² grab	p01g	43.487370	-60.443378	45
Sable Island	1996	Parizeau	P96-009	0.5m² grab	p02g	43.487908	-60.445340	45
Sable Island	1996	Parizeau	P96-009	0.5m² grab	p03g	43.488317	-60.447252	46
Sable Island	1996	Parizeau	P96-009	0.5m² grab	p04g	43.489259	-60.450712	47
Sable Island	1996	Parizeau	P96-009	0.5m² grab	p05g	43.489740	-60.454180	46
Sable Island	1996	Parizeau	P96-009	0.5m² grab	p06g	43.490532	-60.457668	45
Sable Island	1996	Parizeau	P96-009	0.5m² grab	p07g	43.491369	-60.461092	46
Sable Island	1996	Parizeau	P96-009	0.5m² grab	p08g	43.494512	-60.476016	53
Sable Island	1996	Parizeau	P96-009	0.5m² grab	p09g	43.502474	-60.511940	45
Sable Island	1996	Parizeau	P96-009	0.5m² grab	p10g	43.517977	-60.580932	53
Sable Island	1996	Parizeau	P96-009	0.34m sled	p01s	43.480000	-60.440000	46
Sable Island	1996	Parizeau	P96-009	0.34m sled	p02s	43.480000	-60.440000	45
Sable Island	1996	Parizeau	P96-009	0.34m sled	p03s	43.480000	-60.440000	46
Sable Island	1996	Parizeau	P96-009	0.34m sled	p04s	43.480000	-60.450000	47

Sable Island	1996	Parizeau	P96-009	0.34m sled	p05s	43.480000	-60.450000	46
Sable Island	1996	Parizeau	P96-009	0.34m sled	p06s	43.490000	-60.450000	45
Sable Island	1996	Parizeau	P96-009	0.34m sled	p07s	43.490000	-60.460000	46
Sable Island	1996	Parizeau	P96-009	0.34m sled	p08s	43.490000	-60.470000	53
Sable Island	1996	Parizeau	P96-009	0.34m sled	p09s	43.500000	-60.510000	45
Sable Island	1996	Parizeau	P96-009	0.34m sled	p10s	43.510000	-60.580000	53
Western	1997	Parizeau	P97-053	0.5m^2 grab	e01g1	43.749368	-61 68965	72
Western	1997	Parizeau	P97-053	0.5m^2 grab	e03g1	43.748951	-61.690505	71
Western	1997	Parizeau	P97-053	0.5m^2 grab	e06g1	43.747444	-61.689223	71
Western	1997	Parizeau	P97-053	0.5m^2 grab	e08g1	43.746431	-61 689563	70
Western	1997	Parizeau	P97-053	0.5m^2 grab	e11g1	43.745349	-61.689647	71
Western	1997	Parizeau	P97-053	0.5m^2 grab	e16g1	43.742696	-61.690796	70
Western	1997	Parizeau	P97-053	0.5m^2 grab	e18g1	43.741919	-61.689579	69
Western	1997	Parizeau	P97-053	0.5m^2 grab	e?1g1	43.740561	-61.689778	69
Western	1997	Parizeau	P97-053	0.5m^2 grab	e28g1	43.737757	-61.689323	70
Western	1997	Parizeau	P97-053	0.5m^2 grab	e37g1	43.733784	-61.690364	71
Western	1997	Parizeau	P97-053	0.5m^2 grab	b11g2	43.744929	-61 69774	70
Western	1997	Parizeau	P97-053	0.5m^2 grab	b30g2	43.736718	-61 69836	71
Western	1997	Parizeau	P97-053	0.5m^2 grab	g01g2	43.749795	-61 68526	69
Western	1997	Parizeau	P97-053	0.5m^2 grab	g21g2	43.740949	-61 68554	69
Western	1997	Parizeau	P97-053	0.5m^2 grab	g10g2	43.746027	-61 68555	70
Western	1997	Parizeau	P97-053	0.5m^2 grab	i13g3	43.744463	-61 68003	68
Western	1997	Parizeau	P97-053	0.5m^2 grab	i26g3	43.739101	-61 67911	68
Emerald	1996	Parizeau	P96-009	0.5m^2 grab	eb102g	43.340169	-62.279292	81
Emerald	1996	Parizeau	P96-009	0.5m^2 grab	eb105g	43.363073	-62.311037	84
Emerald	1996	Parizeau	P96-009	0.5m^2 grab	eb106g	43.339927	-62.309036	84
Emerald	1996	Parizeau	P96-009	0.5m^2 grab	eb107g	43.330000	-62.300000	83
Emerald	1996	Parizeau	P96-009	0.5m^2 grab	eb1asg	43.348734	-62.309067	83
Emerald	1996	Parizeau	P96-009	0.5m^2 grab	eb201g	43.276621	-62.249888	84
Emerald	1996	Parizeau	P96-009	0.5m^2 grab	eb202g	43.263927	-62.249994	86
Emerald	1996	Parizeau	P96-009	0.5m^2 grab	eb203g	43.000000	-62.270000	88
Emerald	1996	Parizeau	P96-009	0.5m^2 grab	eb208g	43.277939	-62.323221	88
Emerald	1996	Parizeau	P96-009	0.5m^2 grab	eb2asg	43.270000	-62.320000	88
Emerald	1996	Parizeau	P96-009	0.34m sled	eb201s	43.000000	-62.240000	85
Emerald	1996	Parizeau	P96-009	0.34m sled	eb2ass	43.270000	-62.320000	88

APPENDIX II. BENTHIC INVERTEBRATES FROM WESTERN BANK (1997)

Phylum	Genus	Species
Annelida	*Capitella*	*capitata*
Annelida	*Mediomastus*	*ambiseta*
Annelida	*Notomastus*	*latericeus*
Annelida	*Nicomache*	*lumbricalis*
Annelida	*Praxillella*	*praetermissa*
Annelida	Dorvilleidae	
Annelida	*Lumbrineris*	*fragilis*
Annelida	*Nothria*	*conchylega*
Annelida	*Ophelia*	*limacina*
Annelida	*Scalibregma*	*inflatum*
Annelida	*Scoloplos*	*armiger*
Annelida	*Galathowenia*	*oculata*
Annelida	*Owenia*	*fusiformis*
Annelida	*Glycera*	*capitata*
Annelida	*Goniada*	*maculata*
Annelida	*Nephtys*	*caeca*
Annelida	*Nereis*	*zonata*
Annelida	*Eteone*	*longa*
Annelida	*Phyllodoce*	*groenlandica*
Annelida	*Phyllodoce*	*maculata*
Annelida	Phyllodocidae juvenile	
Annelida	*Arcteobia*	*anticostiensis*
Annelida	*Enipo*	*gracilis*
Annelida	*Eunoe*	*nodosa*
Annelida	*Gattyana*	*cirrosa*
Annelida	*Harmothoe*	*imbricata*
Annelida	*Hartmania*	*moorei*
Annelida	*Pholoe*	*minuta*
Annelida	Syllidae	
Annelida	*Chone*	*duneri*
Annelida	*Euchone*	*papillosa*
Annelida	*Jasmineira*	sp.
Annelida	*Apistobranchus*	*typicus*
Annelida	*Spiochaetopterus*	*typicus*
Annelida	*Chaetozone*	sp.
Annelida	*Prionospio*	*steenstrupi*
Annelida	*Spio*	*filicornis*
Annelida	*Ampharete*	*finmarchica*
Annelida	*Pectinaria*	*hyperborea*
Annelida	*Laphania*	*boecki*
Annelida	*Thelepus*	*cincinnatus*
Annelida	*Myxicola*	*infundibulum*
Annelida	*Amphitrite*	*cirrata*
Annelida	*Pholoe*	*tecta*
Annelida	*Harmothoe*	*extenuata*
Annelida	*Nicolea*	sp.

Annelida	*Travisia*	sp.
Annelida	Sabellidae	
Annelida	Maldanidae	
Annelida	*Melina*	*elizabethae*
Annelida	*Eunoe*	*oerstedi*
Annelida	*Aricidea*	sp.
Annelida	*Nicomache*	sp.
Annelida	*Aphrodita*	*hastata*
Annelida	*Orbinia*	sp.
Annelida	*Ophelina*	*acuminata*
Annelida	*Drilonereis*	*magna*
Annelida	*Eunice*	*pennata*
Annelida	*Nephtys*	*discors*
Annelida	*Euphrosine*	*borealis*
Annelida	*Ninoe*	*nigripes*
Annelida	*Pseudopotamilla*	*reniformis*
Annelida	*Tharyx*	sp.
Annelida	*Nephtys*	*ciliata*
Annelida	*Asabellides*	*siberica*
Annelida	*Eulalia*	*bilineata*
Annelida	*Laonice*	*cirrata*
Annelida	*Polydora*	sp.
Annelida	*Polycirrus*	sp.
Annelida	*Aglaophamus*	*circinata*
Annelida	*Myriochele*	*heeri*
Annelida	*Brada*	*granosa*
Annelida	*Chone*	*infundibuliformis*
Annelida	*Flabelligera*	*affinis*
Annelida	*Maldane*	*sarsi*
Annelida	Cirratulidae	
Annelida	*Potamilla*	*neglecta*
Annelida	*Ampharete*	sp.
Annelida	*Eulalia*	*viridis*
Annelida	*Pherusa*	*plumosa*
Annelida	Nephtyidae juveniles	
Annelida	*Petaloproctus*	*tenuis*
Annelida	Scalibregmatidae	
Annelida	*Rhodine*	*loveni*
Annelida	*Praxillura*	sp.
Annelida	*Syllis*	*cornuta*
Annelida	*Exogone*	*verugera*
Annelida	*Exogone*	sp.
Annelida	Syllidae	
Annelida	*Leaena*	sp.
Arthropoda	*Balanus*	*crenatus*
Arthropoda	*Byblis*	*gaimardi*
Arthropoda	*Guernea*	*nordenskioldi*
Arthropoda	*Ischyrocerus*	*megacheir*
Arthropoda	*Anonyx*	sp.

Arthropoda	*Melita*	*dentata*
Arthropoda	*Protomedeia*	*fasciata*
Arthropoda	*Phoxocephalus*	*holboelli*
Arthropoda	*Dyopedos*	spp.
Arthropoda	*Syrrhoe*	*crenulata*
Arthropoda	*Leucon*	*nasicoides*
Arthropoda	*Hyas*	*coarctatus*
Arthropoda	*Pagurus*	*pubescens*
Arthropoda	*Dichelopandalus*	*leptocerus*
Arthropoda	*Munna*	sp.
Arthropoda	*Leptocheirus*	*pinguis*
Arthropoda	*Onesimus*	sp.
Arthropoda	*Ampelisca*	*eschrichti*
Arthropoda	*Acanthonotozoma*	sp.
Arthropoda	*Caprella*	*linearis*
Arthropoda	*Aeginina*	*longicornis*
Arthropoda	*Eualus*	*pusiolus*
Arthropoda	*Photis*	*reinhardi*
Arthropoda	*Leptostylis*	*ampullacea*
Arthropoda	*Eudorella*	*pusilla*
Arthropoda	*Tiron*	*spinferum*
Arthropoda	*Pagurus*	sp.
Arthropoda	*Harpinia*	*serrata*
Arthropoda	*Paroediceros*	*lynceus*
Arthropoda	*Maera*	*danae*
Arthropoda	*Paradalisca*	*cuspidata*
Arthropoda	*Crangon*	*septemspinosa*
Arthropoda	*Janira*	*alta*
Arthropoda	*Dulichia*	sp.
Arthropoda	*Orchomene*	sp
Arthropoda	*Haploops*	*tubicola*
Arthropoda	*Cancer*	*borealis*
Arthropoda	*Monoculodes*	sp.
Arthropoda	Eusiriidae	
Arthropoda	*Dyopedos*	spp.
Arthropoda	*Diastylis*	*quadrispinosa*
Arthropoda	*Leptostraca*	sp.
Arthropoda	*Pagurus*	*arcuatus*
Arthropoda	*Podoceropsis*	sp.
Arthropoda	Haustoriidae	
Arthropoda	*Amphilochus*	*manudens*
Arthropoda	*Amphithopsis*	*longicaudata*
Arthropoda	*Axius*	*serratus*
Arthropoda	*Ericthonius*	*fasciatus*
Arthropoda	*Orchomenella*	sp.
Arthropoda	*Tmetonyx*	sp.
Arthropoda	*Metopella*	sp.
Arthropoda	*Stenothoidae*	sp. A-F
Arthropoda	*Cyathura*	sp.

Brachiopoda	*Terebratulina*	*septentrionalis*
Bryozoa	*Scrupocellaria*	*scabra*
Bryozoa	*Tricellaria*	*gracilis*
Bryozoa	*Dendrobeania*	*decorata*
Bryozoa	*Dendrobeania*	sp.
Bryozoa	*Bugula*	sp.
Bryozoa	*Anasca*	sp. B
Bryozoa	*Ascophora*	sp. A
Bryozoa	*Ascophora*	sp. B
Bryozoa	*Ascophora*	sp. C
Chordata	Ascidiacea (clean)	
Chordata	Ascidiacea (dirty)	
Chordata	Ascidiacea (colonial)	
Cnidaria	Anemone (*Halcampa*-type)	
Cnidaria	Anemone (non-burrowing)	
Cnidaria	*Clavularia*	sp.
Cnidaria	*Lafoea*	sp.
Cnidaria	*Segalinopsis*	*mirabilis*
Cnidaria	Athecate hydrozoa	
Cnidaria	Anemone (*Edwardsia*-type)	
Cnidaria	*Cerianthus*	sp.
Cnidaria	*Sertularella*	*polyzonias*
Cnidaria	*Sertularia*	*mirabilis*
Cnidaria	*Thuiaria*	*lonchitis*
Cnidaria	*Thuiaria*	*articulata*
Cnidaria	*Sertularia*	*schmidti*
Cnidaria	*Lafoea*	*dumosa*
Cnidaria	*Symplectoscyphus*	*tricuspidatus*
Cnidaria	*Rizocaulus*	*verticillatua*
Cnidaria	*Thuiaria*	*alternitheca*
Cnidaria	*Eudendrium*	*ramosum*
Cnidaria	*Thuiaria*	*laxa*
Cnidaria	*Sertularia*	*similis*
Cnidaria	*Lafoea*	*gracillima*
Cnidaria	*Grammaria*	*abietina*
Cnidaria	*Lafoea*	*fruticosa*
Cnidaria	*Halecium*	*labrosum*
Echinodermata	*Strongylocentrotus*	*pallidus*
Echinodermata	Holothuroidea	
Echinodermata	*Psolus*	sp.
Echinodermata	Asteriidae	
Echinodermata	*Ophiopholis*	*aculeata*
Echinodermata	*Ophiura*	*sarsi*
Echinodermata	*Henricia*	sp.
Echinodermata	*Solaster*	*endeca*
Echinodermata	Asteriidae	
Echinodermata	*Crossaster*	*papposus*
Echinodermata	*Spinulosida*	spp.

Echinodermata	*Ophiura*	*robusta*
Echinodermata	*Ophiura*	sp.
Echinodermata	*Amphiura*	sp.
Mollusca	*Crystallophrisson*	*nitidulum*
Mollusca	*Astarte*	sp.
Mollusca	*Cyclocardia*	sp.
Mollusca	*Cyclocardia*	*novangliae*
Mollusca	*Cyrtodaria*	*siliqua*
Mollusca	*Hiatella*	*arctica*
Mollusca	*Macoma*	*calcarea*
Mollusca	*Musculus*	*discors*
Mollusca	Pectinidae	
Mollusca	Gastropoda	
Mollusca	*Margarites*	*striatus*
Mollusca	*Moelleria*	*costulata*
Mollusca	Trochidae	
Mollusca	*Diaphana*	*minuta*
Mollusca	*Philine*	sp.
Mollusca	*Cylichna*	*alba*
Mollusca	*Cryptonatica*	*affinis*
Mollusca	*Neptunea*	sp.
Mollusca	*Polinices*	*pallida*
Mollusca	*Trichotropis*	*borealis*
Mollusca	*Tachyrhynchus*	sp.
Mollusca	*Cerrastoderma*	*pinnulatum*
Mollusca	*Thyasira*	sp.
Mollusca	*Modiolus*	*modiolus*
Mollusca	*Anomia*	*simplex*
Mollusca	*Stenosemus*	*albus*
Mollusca	*Anomia*	*squamula*
Mollusca	*Puncturella*	*noarchina*
Mollusca	*Astarte*	*crenata (subequillateria)*
Moliusca	*Astarte*	*elliptica*
Mollusca	*Crenella*	*glandula*
Mollusca	*Placopecten*	*magellanicus*
Mollusca	*Margarites*	*costalis*
Mollusca	*Thracia*	sp. 1 (short form)
Mollusca	*Thracia*	sp. 2 (long form)
Mollusca	Limpet	
Mollusca	*Bathyarca*	*petunculoides*
Mollusca	Acmaeidae	
Mollusca	*Nudibranchia*	sp. (type 3)
Mollusca	*Antalis*	*entale*
Mollusca	*Nudibranchia*	sp. type 4b
Mollusca	*Astarte*	*undata*
Mollusca	*Nuculana*	sp.
Mollusca	*Calliostoma*	*occidentale*
Nemertea	Nemertea	
Platyhelminthes	Platyhelminthes	

Porifera	Porifera	sp. *(Halichondria* form)
Porifera	*Geodia*	sp.
Porifera	Porifera (sycon)	
Porifera	Porifera	sp. B
Sipuncula	*Phascolion*	*strombi*
Sipuncula	Sipuncula	